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Personalities, social patterns, and reproductive success in female eastern grey kangaroos (*Macropus giganteus*)

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Abstract

Sociality evolves when the benefits of grouping outweigh the costs. Living with relatives can sometimes help to offset some of these costs, and fission-fusion dynamics can help to maximize benefits. Individual differences in sociability can exist and such differences have been linked to fitness consequences in several species. Differences in other personality traits, those that show within-individual consistency and significant differences among individuals, can also influence fitness. However, more research is needed on the relationships among personality traits, and their fitness correlates, in natural populations to better understand the adaptive nature of individual differences in personality traits.

The overall objective of my PhD was to understand some of the constraints, correlates, and fitness consequences of individual differences in sociability in an herbivorous marsupial, the eastern grey kangaroo (*Macropus giganteus*). Eastern grey kangaroos forage in open-membership groups that frequently change in size and composition. Females show natal philopatry but not complex cooperative interactions. I conducted field observations of a wild population of eastern grey kangaroos in Sundown National Park in south-east Queensland, Australia, over more than two years. I documented life-history traits, grouping patterns, and behavioural responses of over 240 identified females, and analysed these data in addition to two previous years' worth of data collected by other researchers.

My first aim (Chapter 2) was to determine the extent to which females' boldness and sociability measures were consistent over multiple years, and how stable correlations among these traits were across time. I also determined whether females' association patterns could be explained to some degree by similarity in boldness, as measured by flight initiation distance. Individual differences in boldness and two measures of sociability (foraging group size and number of preferred associates) were significantly consistent across four years, and correlations between these traits tended to show consistency over time. Some social assortment between females of similar personalities was observed, but this was not consistent over time, and boldness was not related to preferential associations, suggesting that females were not actively choosing to associate with others based on their similarity in personality.

In Chapter 3, I explored the relationships between kinship and association strengths among female kangaroos over four years. I used both biparental genetic relatedness estimates and mother-daughter relationships as measures of kinship, and conducted one set of analyses that considered both adults

and sub-adults, and one restricted to adult females. Both analyses showed weak, yet significant, positive correlations between association strengths and biparental relatedness for all four years. Mother-daughter status of adult females explained almost twice the variation in pairs' association strengths as did biparental relatedness. Although space use overlap explained a high proportion of females' association strengths, controlling for this revealed that a significant relationship between kinship and associations persisted among adult females.

Chapter 4 investigated short-term intrinsic and environmental variables that might constrain the social interactions of adult females. I examined the influences of body condition, reproductive state, food availability, and interactions among these measures, on both aggregation and association patterns of individuals. In months of higher lagged rainfall (a proxy for food availability) females' mean group sizes and the number of different nearest neighbours females had were smaller, while distances between nearest neighbours were larger. Similar to findings from other kangaroo populations, females with larger dependent young foraged in smaller groups, at a greater distance from their neighbours, and grouped with fewer different individuals. Compared to females in poor condition, females in better condition foraged in smaller groups, fed closer to their nearest neighbours when food was plentiful, and had fewer different neighbours.

In Chapter 5 I explored relationships between measures of sociability and female reproductive success, using three approaches that incorporated data across different temporal scales. Parity had a considerable influence on both offspring production and survival at nearly all stages of offspring development - first time mothers had poor success. Contrary to our expectations, the survival of young to weaning was negatively related to several measures of sociability. Females that scored highly on a composite measure of their social network size, and females that had a large number of preferred associates, were less likely to wean a young in a year. At a shorter time scale, the young of females that foraged at closer distances to their nearest neighbours were less likely to survive the period from permanent pouch emergence to weaning.

This thesis contributes to understanding fine- and broad-scale social patterns in a widely distributed gregarious marsupial. Individual differences in sociability, although influenced to some extent by short-term variables, were consistent over time, correlated with females' boldness levels and related to females' reproductive success. The relationships of mothers and their daughters explained the majority of the correlations between kinship and association patterns, although most associations among adults likely occurred between unrelated individuals. Continued research into the individual consistency and fitness consequences of sociability and other personality traits in this population, as

well as in other species, will further our understanding of the importance of these measures from an adaptive perspective.

Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my research higher degree candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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Publications during candidature

Conference Abstracts

Menz, C. S. (2012). *Like Mother, like Daughter? Individual differences in temperament, sociability and space use in the eastern grey kangaroo,* Macropus giganteus. Poster session presented at the Annual Conference of the Australasian Society for the Study of Animal Behaviour, Geelong, Victoria, Australia

Menz, C. S., Best, E. C., Freeman, N. J., Blomberg, S. P., Dwyer, R. G., Goldizen, A. W. (2014). *Individual differences in social connectedness are related to reproductive outcomes in wild female eastern grey kangaroos* (Macropus giganteus). Paper presented at the Annual Conference of the Australasian Society for the Study of Animal Behaviour, Katoomba, New South Wales, Australia

Menz, C. S., Best, E. C., Freeman, N. J., Blomberg, S. P., Dwyer, R. G., Goldizen, A. W. (2014). *Individual differences in social connectedness are related to reproductive outcomes in wild female eastern grey kangaroos* (Macropus giganteus). Paper presented at the 60th Scientific Meeting of the Australian Mammal Society, Melbourne, Victoria, Australia

Goldizen, A.W., Best E. C., Blomberg S. P., Dwyer R. G., Freeman N. J., Menz, C. S. (2015). *More sociable female eastern grey kangaroos are less likely to wean young*. Paper presented at the Behaviour2015 scientific meeting, Cairns, Queensland, Australia

Menz, C. S., Best E. C., Freeman N. J., Goldizen, A. W. (2015). *Kangaroos' boldness relates to their social patterns and assortment*. Paper presented at the Behaviour2015 scientific meeting, Cairns, Queensland, Australia

Publications included in this thesis

No publications included. Chapters 2 through 5 have been written with the intention of submitting them to peer-reviewed journals. I have therefore outlined the contributions of all co-authors to the manuscripts.

Chapter 2 – Menz, C.S., Freeman N. J., Best, E. C., Blomberg, S. P., and Goldizen, A.W. Boldness relates to female kangaroos' sociability and patterns of social assortment.

Contributor	Statement of Contribution
Menz, C. S. (Candidate)	Fieldwork (33%), designed study (50%), statistical analyses (75%), wrote manuscript (100%)
Freeman, N. J.	Fieldwork (33%), edited manuscript (10%)
Best, E. C.	Fieldwork (33%), support in statistical analyses (5%), designed study (25%), edited manuscript (10%)
Blomberg, S. P.	Support in statistical analyses (20%)
Goldizen, A. W.	Project support, designed study (25%), edited manuscript (80%)

Chapter 3 – Menz, C. S., Best, E. C., Freeman, N. J., Seddon, J. M., and Goldizen, A. W. How important is relatedness in structuring female kangaroos' patterns of association?

Contributor	Statement of Contribution
Menz, C. S. (Candidate)	Fieldwork (30%), designed study (50%), molecular genetics work (20%), wrote manuscript (100%)
Best, E. C.	Fieldwork (50%), molecular genetics work (60%), designed study (30%)
Freeman, N. J.	Fieldwork (20%), molecular genetics work (20%), guidance with CERVUS analysis
Seddon, J. M.	Advice and lab support in molecular genetics work, edited manuscript (20%)
Goldizen, A. W.	Project support, designed study (20%), edited manuscript (80%)

Chapter 4 – Menz, C. S., Goldizen, A. W., Freeman, N. J., Blomberg, S. P., and Best, E. C. Intrinsic and environmental predictors of short-term fluctuations in female kangaroos' sociability traits

Contributor	Statement of Contribution
Menz, C. S. (Candidate)	Fieldwork (25%), designed study (10%), compiled data (10%), wrote manuscript (80%)
Goldizen, A. W.	Project support, designed study (50%), wrote manuscript (10%), edited manuscript (80%)
Freeman, N. J.	Fieldwork (40%), compiled data (90%)
Blomberg, S. P.	Advised on statistical models (100%)
Best, E. C.	Fieldwork (35%), designed study (40%), wrote manuscript (10%)

Chapter 5 - C. Menz, E. Best, N. Freeman, R. Dwyer, S. Blomberg and A. Goldizen. Prepared for submission to the *Journal of Animal Ecology*. Reproductive consequences of individual differences in sociability in a large herbivore

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C. Menz (Candidate)	Fieldwork (33%), designed study (50%), wrote manuscript (100%)
E. Best	Fieldwork (33%), designed study (10%), Digiroo2 software support (20%), edited manuscript (10%)
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Contributions by others to the thesis

Since my research relies on shared field data, both Emily Best and Natalie Freeman have made substantial contributions to the thesis in terms of data collection. Emily collected kangaroo field data (including social association surveys, reproductive state and body condition data, and vegetation coverage] from September 2009 until December 2012, and performed experimental tests of kangaroos' flight initiation distance in 2011 and 2012. Emily also genotyped 136 female kangaroos at microsatellite loci from scat collected, and sequenced a mitochondrial DNA segment from of 98 females. Natalie Freeman collected kangaroo field data from March 2012 until November 2014 and assisted with laboratory work to genotype individuals from scat samples. Natalie also assisted in compiling data sets for analysis. Sean Corley assisted with genotyping all the DNA samples for Chapter 3. Paloma Corvalan assisted in collecting both behavioural and genetic data from January to December 2014. Emily Best and Anne Goldizen conceived the idea and analyses and wrote part of an early draft of Chapter 4.

Statement of parts of the thesis submitted to qualify for the award of another degree

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Keywords

Kangaroo, individual differences, personality, sociability, fitness, fission-fusion, social bonds, kinship

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List of Abbreviations Used in the Thesis

AEC- Animal Ethics Committee

ANOVA- Analysis of Variance

BCI- body condition index

bp- base pair (of DNA)

EGK- Eastern grey kangaroo

FID- Flight initiation distance

GLMM- Generalized linear mixed-effects model

GPS- Global Positioning System

Ha- hectares

HWI- Half-weight index

HWIG- Half-weight index controlling for individual differences in gregariousness

ID- Identity

IQR- Inter-quartile range

LPY- large pouch-young kangaroo

m- metres

MGS- Mean Foraging Group Size

MPY- medium pouch-young kangaroo

mtDNA- mitochondrial DNA

NN- Nearest Neighbour

NPY- Female kangaroo with no visible pouch-young

NSW- New South Wales

PCA- Principal Components Analysis

QLD- Queensland

SF- subadult female kangaroo

SNA- Social Network Analysis

SPY- small pouch-young kangaroo

SPY,YAF- Female kangaroo with both a SPY and a YAF

UQ- The University of Queensland

General Introduction

Animal sociality and its benefits and costs

Sociality, or group living, is thought to evolve when the benefits of associating with conspecifics outweigh the costs (Alexander 1974). Benefits can include increased safety from predators, a higher chance of finding a mate and cooperation during hunting or foraging, while costs include increased competition for resources, risk of disease transmission, and risk of infanticide (Krause and Ruxton 2002). The combination of the influences of such benefits and costs is reflected in the sizes of animal groups. Among mammals, the optimal size of a group for the direct fitness of its members can depend on ecological conditions, such as food abundance and predation risk, although such conditions do not influence group size in all instances (Ebensperger et al. 2012). Differences between species in the adaptive benefits of group living can also relate to the extent of cooperative breeding exhibited by species (Silk 2007; Ebensperger et al. 2012). Among cooperatively breeding species, in which young are reared by helpers, group size is often positively related to members' reproductive success (e.g. Clutton-Brock et al. 2001). In species that live in matrilineal groups without communal care of young, increases in matriline size may reduce reproductive success of female members (Clutton-Brock et al. 1982), or initially increase then decrease reproductive success (Armitage and Schwartz 2000), often due to competition and reproductive suppression among related individuals.

Among mammals, males tend to disperse from their natal group or area, while females remain philopatric (Greenwood 1980; Clutton-Brock and Lukas 2012), resulting in members of a group often being maternal relatives. Kinship is an important component of mammalian social evolution, as inclusive fitness theory (Hamilton 1964) suggests that group members can derive indirect fitness benefits through helping or cooperating with relatives. However, closely related group members do not always benefit through inclusive fitness, and cooperation can occur independent of relatedness within a group (Clutton-Brock 2002).

Not all mammal species live in stable groups, with sociality existing on a spectrum from solitary to flexible groups to fixed groups. The spatiotemporal grouping patterns of a species or population allow most societies to be characterised in terms of their fission-fusion dynamics (Aureli et al. 2008). Grouping dynamics in social mammals range along a continuum from species in which group cohesion and memberships are highly stable over time to those exhibiting open membership groups in which individuals frequently join and leave subgroups of varying sizes and composition (Aureli et al. 2008). Higher fission-fusion dynamics, in which individuals frequently join and leave

groups that vary in size and composition, have been described in a number of mammalian species, including, for example, several bats (Kerth and Köing 1999; Patriquin et al. 2010; Ancillotto et al. 2012), Galápagos sea lions (*Zalophus wollebaeki*) (Wolf et al. 2007), African elephants (*Loxodonta africana*) (Wittemyer et al. 2005), bottlenose dolphins (*Tursiops* spp.) (Lusseau et al. 2003), African buffalo (*Syncerus caffer*) (Cross et al. 2005), chimpanzees (*Pan troglodytes*) (Symington 1990), and spotted hyenas (*Crocuta crocuta*) (Holekamp et al. 1997).

Higher fission-fusion dynamics are thought to have evolved as a strategy for coping with unstable environmental conditions in order for individuals to maximise the benefits and reduce the costs of group living under variable circumstances (Lehmann et al. 2007). A number of factors have been shown to influence the size, composition and stability of groups, but much remains to be explored in this area of research. Studies on a range of taxa have demonstrated that resource availability, relatedness among group members, and predation pressure can all influence the fine-scale dynamics of group fissioning and fusioning. Temporal and spatial variability in food resources influence social organisation in populations of spider monkeys (*Ateles geoffroyi*) and chimpanzees (Chapman et al. 1995). In clans of spotted hyena, feeding competition, reproductive state, and degree of within-group conflict all influenced sub-group size (Smith et al. 2008). Groups of female guppies (*Poecilla reticulata*) formed social networks with stronger associations, higher connectivity, and greater temporal stability of dyads when predation risk was higher (Kelley et al. 2011). The fission-fusion dynamics of a group can also be influenced by the relatedness of its members, as seen in African elephants, where adult females typically remained with their close maternal relatives when groups split into multiple smaller groups (Archie et al. 2006).

Although populations with higher fission-fusion dynamics can appear to have little social sub-structure, long-term studies using identified individuals have demonstrated non-random, persistent associations in many such species. Such associations have been reported in some bat species (Patriquin et al. 2010; Kerth et al. 2011), Grevy's zebra (*Equus grevyi*) (Sundaresan et al. 2007), chimpanzees (Langergraber et al. 2009), bottlenose dolphins (*Tursiops* spp.) (Frère et al. 2010b), eastern grey kangaroos (*Macropus giganteus*) (Carter et al. 2009), and giraffe (*Giraffa camelopalardis*) (Bercovitch and Berry 2013; Carter et al. 2013a). The strongest associations within a higher fission-fusion social context often occur between relatives, especially among females where female-biased philopatry occurs. Matrilineal relatedness, in particular relationships between a mother and her daughters, often contributes towards such differentiated social relationships, as seen in bottlenose dolphins (Frère et al. 2010b), red deer (Guinness et al. 1979), mountain goats (Godde et al. 2015), and African elephants (Archie et al. 2006). Females have sometimes been found to closely associate with their female relatives even when the high spatial overlap among kin is

accounted for, as seen in wild boars (*Sus scrofa*) (Podgórski et al. 2014) and giraffe (Carter et al. 2013b).

The influence of kinship on social structure varies widely among species. In addition to recognizing maternal relatives through familiarity, in some species individuals are also able to distinguish paternally-related kin, even when the mating system suggests that paternity should be cryptic (Widdig 2007). Inclusive fitness theory predicts that individuals should preferentially associate or interact with paternal half-siblings, which are on average as closely related to an individual as their maternal half-siblings, if they derive a fitness benefit from such relationships (Hamilton 1964). Although behavioural bias towards paternal kin has indeed been described in some primates with stable and cohesive group membership (Smith et al. 2003; Perry et al. 2008; Schülke et al. 2013), the extent to which animals favour their paternal kin (over unrelated individuals) is not well described in species within higher-fission fusion dynamics. Rates of some social interactions, but not others, differed between paternal half-sibling pairs and unrelated pairs of spotted hyenas (Wahaj et al. 2004), but chimpanzee paternal half-brothers did not show preferences for affiliating or cooperating (Langergraber et al. 2007). In other species with higher fission-fusion dynamics, associations can also be unrelated to either maternal or paternal kinship. For example, the stable and non-random associations formed by southern flying squirrels (*Glaucomys volans*) when nesting were not predicted by genetic relatedness of pairs (Garroway et al. 2013). Common raccoons (*Procyon lotor*) in a high-density population also exhibited strong social preferences that were unrelated to kinship despite the presence of close relatives in the population (Hirsch et al. 2013), while relatedness did not predict females' roosting associations in colonies of big brown bats (*Eptesicus fuscus*) (Metheny et al. 2008).

Individual differences in sociability

Within animal populations, individuals of the same sex, age, or size class often differ in their behaviour, with these differences reflecting personality traits (Réale et al. 2007). Personality, or temperament, is broadly defined as between-individual differences and within-individual consistency in behaviour over time. Understanding how individual differences in personality types are both generated and maintained within a population has been a growing area of interest for behavioral ecologists over the past decade (Stamps 2007; Dingemanse and Wolf 2010; Réale et al. 2010; Wolf and Weissing 2010; Wolf and McNamara 2012). Personality traits explained approximately a third of variation in behaviour among individuals in a meta-analysis of 114 studies (Bell et al. 2009), are often heritable (Stirling et al. 2002; van Oers et al. 2005) and can have

consequences for fitness (Biro and Stamps 2008; Smith and Blumstein 2008). Within populations, personality traits that are consistently correlated across situations comprise a 'behavioural syndrome' (Sih et al. 2004), although the strengths of such correlations can vary with environmental conditions (Garamszegi et al. 2013). Behavioural syndromes imply that behavioural plasticity can be evolutionary constrained, and that individuals may not display optimal behaviour in a given situation.

Five broad dimensions to animal personality are often studied: boldness, exploratory tendency, aggressiveness, activity, and sociability (Réale et al. 2007). Different studies have quantified sociability in different ways depending on the extent of gregariousness or cooperative behaviour within a species. These sociability measures can reflect quite different aspects of an individual's behaviour – such as gregariousness, numbers of associates, and strengths of social bonds – and there is little known about whether these measures represent facets of a single personality trait or whether they are separate traits (Koski 2014). In semi-social species, tolerance of the odour of conspecifics can reflect sociability (Cote and Clobert 2007). In gregarious animals without cooperative interactions, preferred group sizes (Cote et al. 2012), distances to nearest neighbours (Sibbald et al. 2005), and propensity to approach conspecifics (Kohn et al. 2013), among other behaviours, have been used as measures of sociability. Social network analysis metrics can also be used to look at individuals' integration into the network as a whole, and are able to consider direct and indirect connections to other animals (Whitehead 2008). In species with complex cooperative interactions, individuals' sociability is often quantified using a composite score based on several, often highly correlated, behaviours. Such composite scores may combine measures of proximity to neighbours, frequency of grooming, and affiliative approaches to others, as has been done for primates (Silk et al. 2003; Silk et al. 2010b) and feral horses (*Equus caballus)* (Cameron et al. 2009). Principal components analysis has also been used to collapse several measures of sociability, including social network metrics, into a smaller number of uncorrelated variables (Wey and Blumstein 2012; Fuong et al. 2015).

Sociability can have important consequences for individuals' fitness. Many studies have highlighted the importance of stable social relationships for health and wellbeing in humans (House et al. 1988; Hawkley and Cacioppo 2010; Holt-Lunstad et al. 2010), and social integration has also been found to have fitness consequences in non-human animals (reviewed by Silk 2007; Seyfarth and Cheney 2012). The first evidence of the adaptive value of close social relationships in animals came from a long-term study of wild savannah baboons (*Papio cynocephalus*), a species with matrilineal dominance hierarchies in which females can have strong affiliative bonds with one another (Silk et al. 1999). Females who scored highly on a composite sociability index composed of measures of

grooming and the maintenance of proximity to other adults experienced greater offspring survival to one year of age (Silk et al. 2003). Another study of chacma baboons (*Papio cynocephalus ursinus*), a closely related species, focused specifically on social bonds among adult females and also reported higher infant survival for females with the highest composite sociability scores (i.e. those that formed the strongest bonds with other females, Silk et al. 2009). Female chacma baboons also exhibit close and persistent social bonds with one another (Silk et al. 2010a), and individuals with the strongest social bonds experienced increased longevity (Silk et al. 2010b). In addition to relationships with other females, social bonds with males can also benefit female survival in savannah baboons (Archie et al. 2014). Evidence also exists of individuals in captive primate populations receiving fitness benefits from social integration. In a semi-free ranging population, juvenile female mandrills (*Mandrillus sphinx*) who engaged in more affiliative interactions reproduced for the first time at younger ages than did less socially integrated females (Charpentier et al. 2012), while captive female western lowland gorillas (*Gorilla gorilla gorilla*) scoring highly on a personality dimension for extraversion (a trait correlated with higher rates of affiliation) lived longer than introverted females (Weiss et al. 2013).

In species with female-biased philopatry, the benefits of sociability can be difficult to separate from the benefits of associating with close relatives. However, recent studies have demonstrated that close social relationships with non-relatives can also have direct fitness consequences for females. Female feral horses live in stable groups with have low relatedness among adult females, yet more socially integrated females had higher birth rates and survival of foals (Cameron et al. 2009). In bottlenose dolphins the reproductive fitness of a female's preferred associates was the strongest predictor of her own calving success when female pairs had low relatedness (Frère et al. 2010a). Social centrality also influenced survival and offspring production in female bighorn sheep (*Ovis canadensis*), a species with higher fission-fusion dynamics in which individuals do not live in kin-structured groups (Vander Wal et al. 2015).

Despite the benefits that being sociable can offer, several studies have also demonstrated that high sociability can be costly for fitness in some instances. In a colonial burrow-dwelling rodent, the yellow-bellied marmot (*Marmota flaviventris*), individual females with weak social affiliations experienced greater annual reproductive success than did more socially integrated females (Wey and Blumstein 2012). Female red-necked wallabies (*Macropus rufogriseus*) that grouped more frequently with females in their matriline had reduced infant survival rates (Johnson 1986), and red deer hinds belonging to larger matrilineal groups also had lower reproductive success (Clutton-Brock et al. 1983). However, these studies all involve sociability in the context of interactions with kin, which raises the possibility that social integration may relate to inclusive fitness benefits

(Hamilton 1964) even if it results in a cost to individuals' direct fitness. There is very little known about whether being more sociable than other individuals may be costly for reproductive success in social species that have little or no kin structure in their grouping patterns.

It is increasingly recognised that social integration beyond the level of dyadic relationships may be another important component of an individual's overall sociability, and may have consequences for fitness and social transmission of information (reviewed by Brent 2015). Social network analysis techniques have been increasingly adopted in ecological and animal behaviour research in recent years (Berman et al. 1997; Krause et al. 2007; Wey et al. 2008; Krause et al. 2009; Sih et al. 2009; Burt et al. 2013; Kurvers et al. 2014), and this approach allows researchers to study an individual's integration within the population beyond the level of the dyad. Measures for individuals describing different aspects of their connectedness within a network can be derived from social network analysis, allowing indirect connections as well as direct connections to be quantified. Indirect connections, or 'friend of a friend' relationships, are being increasingly recognized as having important consequences for information transfer and social learning (Brent 2015). The use of social network analysis in animal populations has allowed quantification of an individual's position in the group or population that would not have been possible using pairwise measures of associations/interactions alone. In free-ranging rhesus macaques (*Macaca mulatta*), both males and females that scored highly on a proximity-based social network measure of indirect connectedness (measuring the degree to which they associated with individuals who themselves spent time associating with others) produced the greatest number of offspring that survived to one year of age (Brent et al. 2013a). Similarly, juvenile male bottlenose dolphins with a higher tendency to associate with other highly socially integrated individuals had a greater probability of survival (Stanton and Mann 2012), likely due to such individuals' network positions providing a social buffer against harassment.

The population-level properties of a social network can also have outcomes for the fitness of individuals within the network, even when there are no fitness consequences related to individuals' own positions within the network. For example, in the plural breeding rock hyrax (*Procavia capensis*), animals from groups that had more egalitarian associations had greater longevity than groups in which some individuals were significantly more socially central than others, although individual measures of social centrality did not predict longevity (Barocas et al. 2011). A similar outcome for female reproductive success was reported in degus (*Octodon degus*), also pluralistic breeders, where group-level reproductive output was higher for groups in which members'

association strengths were all similar, compared to groups with heterogeneous association strengths (Wey et al. 2013).

The mechanisms by which social bonds can increase fitness in group-living mammals are still not fully understood. Social integration may provide a buffer against stressful social situations within a group, allowing individuals with stronger social bonds to better cope in times of stress. Indeed, several studies in primates have shown that females with strong social relationships had lower chronic stress levels than did less sociable females (Crockford et al. 2008; Silk et al. 2010b; Brent et al. 2011). Social integration may also mediate the effects of non-social or environmental stressors, as wild female vervet monkeys (*Chlorocebus pygerythrus*) with a greater number of social relationships were better able to maintain their core body temperature in cold conditions (McFarland et al. 2015). In non-primate species, there is less known about how fitness advantages may be conferred through individuals' sociability. The increased reproductive success and offspring survival in female feral horses that were more socially integrated (Cameron et al. 2009) may have been partially attributable to the reduced male harassment these females experienced. Similarly, in a captive population of catsharks (*Scyliorhinus canicula*), females with strong and stable connections in the social network were less disturbed by harassment from male intruders than were females with weaker social connections (Jacoby et al. 2010). Animals may also derive foraging benefits from associating with their preferred social partners. Female eastern grey kangaroos that grazed with a frequent associate were less vigilant (and consequently could devote more time to feeding) than when grazing with a less familiar conspecific (Carter et al. 2009), although the reason for this is still unclear.

Despite individual differences in sociability having been reported in many species, and increasing evidence that such differences can relate to fitness outcomes in mammals, there is little known about how social bonds (or 'friendships', Seyfarth and Cheney 2012) among females have evolved. Research on the adaptive nature of social bonds has mainly focused on species with complex social systems and cooperative interactions. However, we know that in some social species without such cooperative behaviours – where individuals do not cooperate in foraging or rearing young, groom one another, or form competitive alliances – females can develop close and persistent social relationships, so it is likely that social bonds arose before such complex behaviour evolved. Although the general benefits of grouping are well established (Krause and Ruxton 2002), having close relationships with particular other individuals differs from merely aggregating. Although some recent research is beginning to address the fitness outcomes of sociality bonds among non-cooperative social mammals in the wild – for example, a long-term study by Vander Wal et al.

(2015) on bighorn sheep – more studies like this are needed to begin to understand the evolutionary significance of social bonds.

Individual differences in other personality traits

The continuum from bold to shy temperament, also referred to as risk-taking to risk-aversion, is one of the most well-researched facets of animals personality (Wilson et al. 1994). Repeatable and heritable individual differences in boldness have been described in captive-bred and wild populations of great tits (*Parus major*) (Dingemanse et al. 2002; Drent et al. 2003; Carere et al. 2005), several social fish species (Chevert et al. 2011), and bighorn sheep (Réale et al. 2000; Réale and Festa-Bianchet 2003; Réale et al. 2009), among other species. Individual variation in boldness has been linked to differences in behaviours that are important for fitness in the wild (reviewed by Dingemanse and Réale 2005; Smith and Blumstein 2008). In several vertebrates, boldness has been found to consistently relate to other personality traits, often forming a behavioural syndrome (Sih et al. 2004) where individuals' personalities fall somewhere on the 'reactive-proactive' scale, in which levels of boldness, exploration tendency, and aggressiveness are closely correlated (Koolhaas et al. 1999; Réale et al. 2007). Boldness has also been found to relate to several aspects of sociability, including aggregation tendency (Ward et al. 2004; Best et al. 2015), propensity to leave or change groups (Pike et al. 2008; Michelana et al. 2009), and social foraging strategies (Kurvers et al. 2010). However, there is no consistent pattern across species in the relationship between boldness and sociability, perhaps due to the variety of ways in which both sociability and boldness have been quantified or tested.

The majority of experimental studies of animal personality have either been conducted on captive populations in a laboratory environment, or on wild-caught animals that are temporarily moved to controlled settings for testing. Quantification of individual behavioural types in wild populations has typically relied on observational data from focal animal sampling (Altmann 1974) (for example, Twiss and Franklin 2010; Seyfarth et al. 2012; Brent et al. 2013b; Jennings et al. 2013), although other studies on wild populations have quantified an animal's response to capture or handling in the field (Réale et al. 2000; Petelle et al. 2013). Testing individual differences in temperament in wild animals in their natural environments can be logistically difficult, due to lack of control over external variables that might influence an animal's behaviour. It can also be difficult to present a standardized stimulus to an individual to elicit the behaviour of interest without affecting other members of the population. Despite such challenges, research on wild populations is crucial for understanding how animals express their individual differences in the wider ecological and social context in which these differences have evolved (Archard and Braithwaite 2010). Although traits

measured in captivity can be highly correlated with their analogous traits in the wild (Herborn et al. 2010), this is not always the case (McCowan et al. 2015), and researchers are increasingly becoming aware of the need to validate whether personality traits measured in captive environments accurately reflect ecologically significant traits in the wild (Niemelä and Dingemanse 2014). The use of targeted, in-field tests to elicit a measurable behavioural response from individuals without capturing or handling them is rare, but such methods have been used for several species, including grey seals (*Halichoerus grypus*) (Twiss et al. 2011), eastern grey kangaroos (Best et al. 2015), and chacma baboons (Carter et al. 2012). The social contexts in which animals express their personalities are also beginning to receive closer attention (Webster and Ward 2011). Recent empirical studies have shown that individuals in captivity can respond differently when tested for personality traits in different social contexts. For example, male cichlid fish (*Oreochromis mossambicus*) showed more exploratory behaviour in the presence of a familiar conspecific than males tested in isolation or in the presence of an unfamiliar fish (Galhardo et al. 2012), while zebra finches (*Taeniopygia guttata*) were less exploratory in the presence of conspecifics (Mainwaring et al. 2011).

Homophily and social assortment based on similarity in temperament have been described in a number of species. Wild-caught guppies showed social assortment in their social networks by behavioural phenotype, with bolder fish having strong network connections to other bold animals (Croft et al. 2009). In a large-scale social network study of wild great tits that tested birds' exploratory behaviour, males tended to associate with individuals of similar personality at both network-wide and feeding group levels (Aplin et al. 2013). Assortment by personality type can also occur at the dyadic level in a social network, as demonstrated in a study on captive chimpanzees. Friendships between individuals, as determined by how frequently a pair sat in physical contact with one another, were based at least in part on similarity in the personality dimensions of boldness and sociability (Massen and Koski 2013). Similarity in temperament of pairs of infant rhesus macaques (*Macaca mulatta*) predicted their affiliative relationships as yearlings, even after sex, kinship and rank were considered (Weinstein and Capitanio 2008). Individual captive brown capuchin monkeys (*Sapajus apella*) with similar observer ratings on the neuroticism and sociability personality dimensions were more affiliative and had higher quality relationships, respectively, with one another than did pairs with less similar personalities (Morton et al. 2015). In free-ranging horses (*Equus ferus caballus*), individuals associated more strongly with conspecifics who had similar boldness scores to them (Briard et al. 2015).

Why individuals that are similar in personality would also have closer associations, or higher quality social bonds with each other, is not clear, and has not been investigated in the above studies.

Individuals may seek out social partners that are similar in temperament to them (homophily, as reviewed by McPherson et al. 2001); alternatively, social conformity may cause individuals to become increasingly similar in temperament the more time they spend with one another (Webster and Ward 2011; King et al. 2015a). A spatial or habitat component may also play a role in explaining observed patterns of social assortment (Krause et al. 2010). Individuals with different temperaments may use their habitat in different ways (for example, shyer individuals may prefer to feed closer to cover), which could result in individuals pairing or aggregating because they both prefer the same habitat or conditions (Croft et al. 2009). Whatever the causes of such patterns, understanding how personality measures relate to social context is likely to continue to be an area of interest for behavioural ecology.

Study species: the eastern grey kangaroo

The eastern grey kangaroo is a large-bodied grazing macropod with a widespread and continuous distribution throughout the eastern states of mainland Australia and north-eastern Tasmania (Poole 1982). Eastern grey kangaroos share a number of behaviours with grazing ungulate species and are often considered their ecological equivalents (Jarman 1983). Macropods, like other marsupials, have a short gestation period compared to placental mammals of similar body weight. Eastern grey kangaroos give birth after 36 days gestation (Poole 1982), after which the young migrates to the pouch and latches onto a teat where it continues to suckle and develop. Approximately 46 weeks after birth, the young permanently emerges from the pouch, although temporary exits from the pouch begin about 1 - 2 months prior to this date. After permanent emergence from the pouch, young (known as 'young-at-foot' at this stage in development) continue to nurse for 7 to 8 months before they are weaned (Lee and Ward 1989) and closely follow their mothers while grazing, similarly to the young of some ungulate species with 'follower' strategies (Fisher et al. 2002). Once her young leaves the pouch, a female can give birth to another young when she has a dormant blastocyst stored. Females generally produce an average of one young per year, although when food is abundant and conditions are good this inter-birth interval may be shorter (Stuart-Dick 1987). Although females have been reported to commence breeding as early as 17 months of age, mean age at first conception is usually around 22 months in wild populations, but this varies with conditions and between individuals (reviewed by Stuart-Dick 1987). Eastern grey kangaroos reproduce throughout the year, although seasonal peaks of pouch emergence can occur when environmental conditions are favourable (Poole 1983; Stuart-Dick 1987).

Eastern grey kangaroos graze in open-membership groups that frequently change in size and composition (Southwell 1984c). Foraging in groups is thought to be an adaptive response to

predation (Jarman and Coulson 1989), and group sizes can vary depending on predation risk (Banks 2001). Average group sizes have been estimated in various populations to range from 1.8 to 12.5 animals, and vary with population density and with habitat structure (Southwell 1984b; Coulson 2009). The mean 'typical' group size (group size experienced by an average individual) has been reported as ranging from 2.4 to more than 20 animals (Southwell 1984a; Jarman and Coulson 1989). Historical observations suggested that individual kangaroos joined and left groups at random and that social structure was largely absent, except for the tendency for offspring to remain close to their mothers following weaning (Caughley 1964; Kirkpatrick 1966; Grant 1973). Later studies, however, suggested that individuals inhabiting the same area might exist in loosely structured yet discernable communities (Kaufmann 1975; Stuart-Dick 1987; Jaremovic and Croft 1991). Kaufmann (1975) proposed that individuals may belong to 'mobs' that separated into smaller groups when foraging, and whose members associated with each other more often than with members of other mobs. Observations on individually identified animals confirmed this tendency for more frequent within-mob than between-mob associations, despite all animals grazing within the same study area (Jaremovic and Croft 1991). In my study population at Sundown National Park in Queensland, social network analysis separated females statistically into communities, where individuals within a community associated more frequently with each other than with females from other communities (Best et al. 2013b). Although kangaroos exhibit high fission-fusion dynamics in their grouping behaviour, females' association patterns can be non-random and a show a high degree of social differentiation (Best et al. 2013b). Preferred associations (and avoidances) have been documented between adult female kangaroos, defined as pairs that associate more (or less) frequently than expected based on their degree of foraging range overlap (Carter et al. 2009; Best et al. 2014). Weaker association strengths among females were found in a population at high density (King 2015) than those reported in the Sundown National Park study, suggesting that population density is a key variable in determining social structure in this species.

Stuart-Dick (1987) suggested that a matrilineal social organisation might be present in eastern grey kangaroos, based on observations that males dispersed but daughters tended to be philopatric upon reaching maturity. Long-term observational studies of kangaroo populations have reported that mothers and daughters (and to a lesser extent and for a shorter period of time, also mothers and sons) continue to associate after weaning, and young females often remain within their mother's range for several years (Grant 1973; Stuart-Dick 1987; Stuart-Dick and Higginbotton 1989; Jarman 1994). Mothers and their adult daughters at a study site in Wallaby Creek, New South Wales, were found grouped together approximately 25% of the time (Stuart-Dick and Higginbotton 1989). Male-biased dispersal has also been demonstrated with genetic analyses (Zenger et al. 2003; Coghlan

2013; King et al. 2015b) and behavioural observations (King et al. 2015b). However, studies in two populations of eastern grey kangaroos have shown that while weak genetic structuring existed at a fine spatial scale, meaning that females whose core foraging ranges were geographically close were more likely to be related (Best et al. 2014), kinship was not strongly correlated with association patterns in these populations (Best et al. 2014; King et al. 2015b). In addition, although females within a community were more closely related than the population average, these communities did not represent matrilines (Best et al. 2013b).

Study site and population

My research was undertaken at a 37.4-hectare study site in the southwest corner of Sundown National Park, on the border of Queensland and New South Wales, Australia (28°55'03''S, 151°34'46''E; Figure 1). The site is a patchwork of grassy paddocks and open woodland with silver-leaved ironbarks (*Eucalyptus melanophloia*) and cypress pines (*Callitris indatropica*) the dominant tree species. The Severn River, which was alternately dry or flowing depending on local rainfall during the study period, delineates the southern border of the site. Although the park lacked dingos (*Canis lupus dingo*), which can prey on adult kangaroos, red foxes (*Vulpes vulpes*), known predators of juveniles, were occasionally see within the study area. Another potential predator of young kangaroos, wedge-tailed eagles (*Aquila audax*) were occasionally observed flying over the study area.

The eastern grey kangaroo population within the study site has been observed by researchers since 2009, and has become habituated to the presence and movements of researchers. The population has been the subject of research into population social structure (Best et al. 2013b; Best et al. 2014), vigilance behaviour (Favreau et al. 2010; Favreau et al. 2015), individual personalities (Lim 2009; Dannock et al. 2013; Edwards et al. 2013; Favreau et al. 2014; Best et al. 2015), and geophagy behaviour (Best et al. 2013a). Between 2010 and 2014, approximately 240 adult and sub-adult female kangaroos regularly grazed in the study area each year, with over 290 different females recorded within the site during these years. A smaller number of sub-adult and adult males used the site each year, although males were not individually identified for the current study. Females were recognized based on their natural features and markings, as described previously for this and other populations (Jarman et al. 1989; Carter et al. 2009; Best et al. 2013b).

Thesis outline and objectives

My research had two broad objectives. First, I investigated variables that related to associations among females within the population. Second, I looked at potential causes of individual differences in females' sociability, and the reproductive consequences of these differences. I personally collected data in the field over 24 months on the social patterns, life history traits, and behavioural measures of the population of eastern grey kangaroos at Sundown National Park. I was able to use an additional 24 months' of the same kinds of data collected prior to my data by another researcher (Dr. Emily Best), and 12 months of data collected afterwards (by Paloma Corvalan and Natalie Freeman) in order to undertake analyses that looked at longer-term patterns. The thesis is written as a series of manuscripts for publication in peer-reviewed journals, hence there is some repetition in the methods sections, and each chapter has its own discussion section. Chapters 2, 3, and 4 have not yet been formatted for particular journals, but Chapter 5 has been written and formatted with the intention of submitting it to the Journal of Animal Ecology. The specific objectives of each thesis chapter are described below.

In Chapter 2, I quantify the long-term consistency of individual differences in the personality dimensions of boldness (risk-taking) and sociability, and the persistence of a previously suggested behavioural syndrome between these traits, across multiple years. I also test whether females' association patterns reflect social assortment and social preferences based on similarity in boldness.

Chapter 3 determines the contributions of biparental genetic relatedness and maternal kinship to yearly association strengths among females, considering associations among both sub-adult and adult females, and among adult females only. Overlap in pairs' foraging range patterns was also considered in these analyses to look at how genetic relatedness may contribute to preferential associations.

Chapter 4 explores the degree to which temporally unstable variables, both intrinsic and environmental, might relate to females' social patterns in the short term. I consider the influences of these factors on patterns of both aggregations and females' associations with particular individuals, to explore the constraints on different aspects of females' sociability.

In Chapter 5 I use multiple approaches, including social network analysis, to quantify different aspects of females' sociability over the long term, and investigate the consequences of individual differences in these sociability traits on the production and survival of young. Three temporal scales are considered when looking at reproductive success.

Finally, in Chapter 6, I integrate the findings from Chapters 2 to 5 and discuss my results across chapters in the context of other studies and theories. I also address some limitations of the work and suggest areas for future research.

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Figures

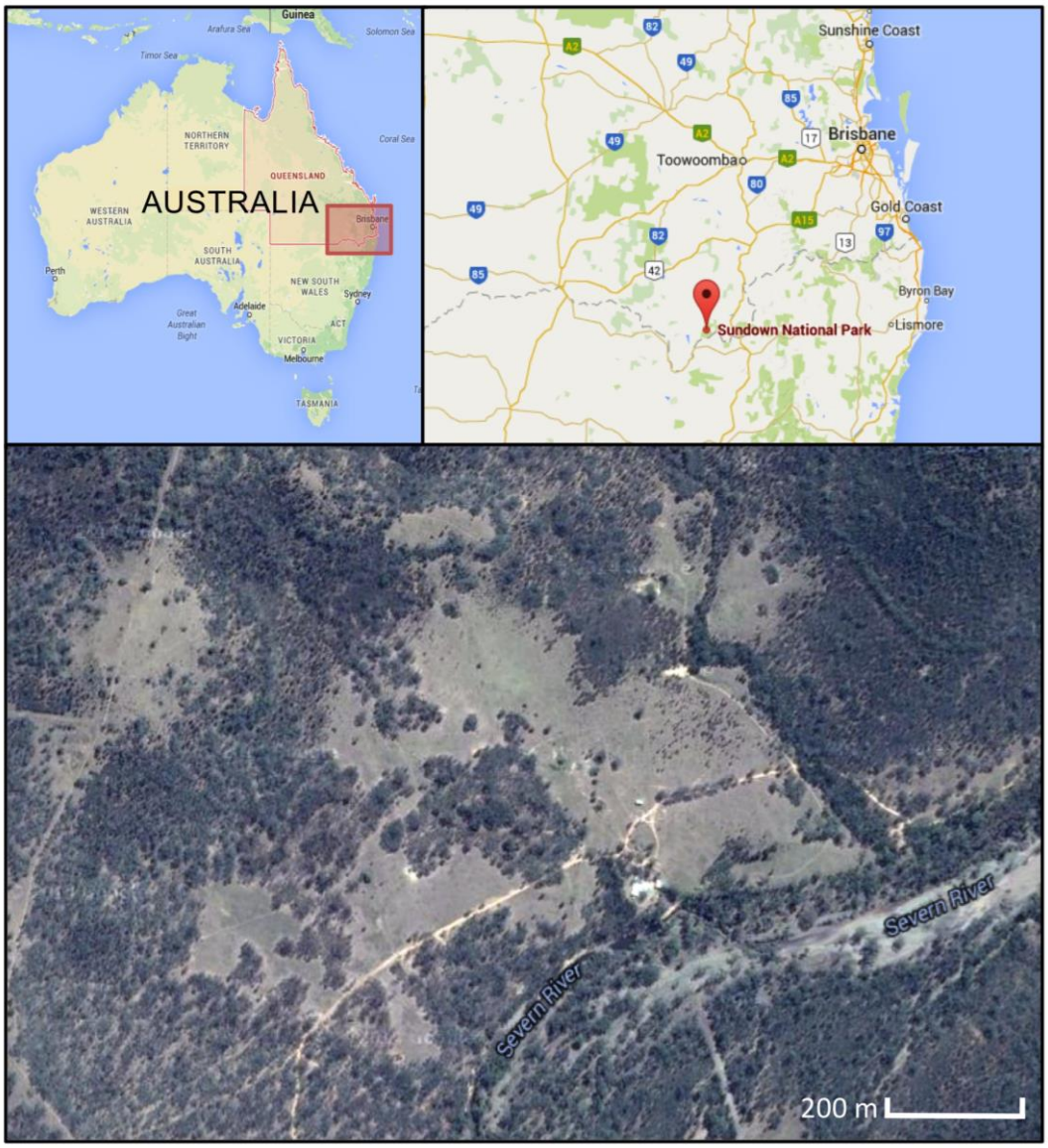

Figure 1. Map showing the location of Sundown National Park, with an aerial view of the study area. All map images from Google.

Boldness relates to female kangaroos' sociability and patterns of social assortment

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Abstract

Consistent individual differences in behaviour (called personality or temperament) have been described in a wide range of taxa in both wild and captive populations, and are increasingly considered to be of ecological and evolutionary significance. Boldness/shyness, or risk-taking/risk-aversion, is a dimension of animal personality that has been investigated in a large number of empirical studies of different species. However, the relationship between boldness and sociability, a less-studied axis of personality, does not show consistent patterns among species, perhaps at least partly because sociability can be measured in many different ways. There has also been little research on whether relationships between these two personality axes remain stable over long time periods or across varying environments. Our four year study of a wild population of over 200 individually identified eastern grey kangaroos (*Macropus giganteus*) has provided a model system in which to explore how individuals' boldness relates to various metrics of their sociability, and the consistency of these relationships across time and changing environmental conditions. We previously reported consistent individual differences in boldness and in measures of sociability, and showed that bolder individuals foraged in smaller groups, and formed preferential associations with more conspecifics, than did shyer animals. Here we show that boldness and sociability are consistent over a much greater time period, and that the previously described relationship between boldness and sociability also remained consistent despite changes in the physical and social environments of the population. In addition, we investigated the extent to which similarity in boldness explained females' pairwise association strengths. A moderate degree of social assortment based on similarity in boldness was observed, although this was not consistent between testing periods and was not related to preferential pairwise associations. These findings show that female kangaroos' boldness levels are tightly linked to their social patterns, and provide further support for a boldness-sociability behavioural syndrome in this population.

Introduction

The ecological and evolutionary significance of temperament in animal populations has been a growing area of interest in recent years. It is now widely accepted that individuals in many species

differ consistently in their behaviour, and that these individual differences, variously termed animal personality (Gosling 2001), temperament (Réale et al. 2007), or coping style (Koolhaas et al. 1999) and often have a significant heritable component (Dingemanse et al. 2002; Drent et al. 2003; MacColl and Hatchwell 2003; Bize et al. 2012; Ariyomo et al. 2013; Brent et al. 2013b). Five broad axes of animal personality have been proposed to exist across taxa – boldness, exploratory tendency, sociability, activity, and aggressiveness (Réale et al. 2007) – although personality researchers are being increasingly encouraged to look beyond this paradigm when considering which behaviours fit the criteria for personality traits (Koski 2014). The evolutionary processes that generate and maintain individual differences and within-individual consistency in personality types have been a key topic for personality researchers over the past decade. Various theories addressing this question have been proposed (Dingemanse and Wolf 2010), including (for example) feedback between states and behaviour (Wolf and Weissing 2010; Sih et al. 2015), links to life-history trade-offs (Biro and Stamps 2008), and spatio-temporal variation in fitness of different personality types (Wolf and Weissing 2010). Another hypothesis for how different personality traits can coexist in a group or population suggests that repeated social interactions with conspecifics may drive individuals to develop 'social niches' - alternative behavioural options that reduce social conflict and competition for resources (Bergmüller and Taborsky 2010; Montiglio et al. 2013).

The continuum from bold to shy temperament, also referred to as risk-taking and risk-aversion, has been one of the most well-researched facets of animal personality (Wilson et al. 1994). Consistent individual differences in boldness have been described in a number of taxa, in both captive and wild populations (e.g. Ward et al. 2004; Cote et al. 2010; Carter et al. 2012a; Massen et al. 2013). Boldness has also been found to correlate with life-history traits that are important for fitness in the wild, such as dispersal and reproductive success (reviewed by Dingemanse and Réale 2005; Smith and Blumstein 2008). Research on bighorn sheep (*Ovis canadensis*) has demonstrated the evolutionary significance of individual variation in boldness among wild mammals. Boldness is positively related to reproductive success in females (Réale et al. 2000) and in older males (Réale et al. 2009), and thought to confer selective advantage against predation (Réale and Festa-Bianchet 2003). Bolder individuals are often consistently more aggressive (Huntingford 1976; Riechert and Hedrick 1993) and have greater exploratory tendency (Smith and Blumstein 2010; Wisenden et al. 2011) than shyer animals. Within populations, temperament traits that are correlated across contexts and situations – known as behavioural syndromes (Sih et al. 2004) – may derive from the same proximate mechanisms and can be constrained in evolving independently from one another (Dall et al. 2004; Sih et al. 2004), limiting individuals' behavioural plasticity.

Despite being considered one of the five broad axes of animal personality (Réale et al. 2007), sociability has not been extensively studied as a personality trait or set of traits. Individual differences in sociability have been linked to consequences for reproductive success and fitness in a number of species (Silk et al. 2003; Cameron et al. 2009; Wey and Blumstein 2012), so it is likely that sociability is an ecologically and evolutionarily significant aspect of temperament. Individuals' sociability has been quantified in a variety of ways across different species, with the measure of sociability used depending in part on the social complexity of the study population. Some measures of sociability have been based on an individual's grouping and proximity preferences (Sibbald et al. 2005; Cote et al. 2012), while other studies have measured the numbers and strengths of an individual's social connections with conspecifics (Croft et al. 2005; Pike et al. 2008). Studies of species with complex social interactions often combine several measures of affiliative behaviour into a composite sociability index (Silk et al. 2003; Smith et al. 2003; Cameron et al. 2009; Silk et al. 2010). Sociability of individuals can also be described in terms of their positions in the social network of the population (Wilson et al. 2013), with this kind of analysis allowing for indirect as well as direct associations to be quantified. It has been suggested that social network positions could themselves fit the criteria for personality traits (Krause et al. 2010), and social network tendencies have been shown to be repeatable over time (Best et al. 2015), have some degree of heritability (Brent et al. 2013a), and be under selection (Lea et al. 2010).

The majority of experimental studies of individual variation in personality have either been conducted on captive populations in a laboratory setting, or on wild-caught animals that were temporarily moved to controlled settings for testing. Although studies have also been undertaken on wild animals in their natural environments for a number of species (e.g. Réale et al. 2000; Martin and Réale 2008; Carter et al. 2012b; Petelle et al. 2013), this approach is less common, and can present logistical difficulties such as lack of control over environmental variables. However, such studies are necessary to understand how animals express their individual differences in the wider ecological and social context in which they have evolved (Archard and Braithwaite 2010). Although individuals' traits measured in captivity can be highly correlated with their analogous traits in the wild (Herborn et al. 2010), it is still uncertain whether animal personality tested in captive environments accurately reflects ecologically significant traits in the wild. Validating laboratory-measured individual differences in the wild, and studying wild populations in their natural environment, are crucial to understand the ecological validity and adaptive nature of this variation (Niemelä and Dingemanse 2014).

Group-living species perform their behaviours in a social environment, so it is important to study individual differences in behavioural types in the social environment in which they evolved (Sih et al. 2004; Réale et al. 2007; Bergmüller and Taborsky 2010). Animals may express their personality traits differently when tested in isolation than when tested in a more natural social setting, as was seen in a recent study on zebra finches (*Taeniopygia guttata*), in which individuals were less exploratory when tested in the presence of conspecifics (Mainwaring et al. 2011). The combination of different personality types within a group can influence group-wide social structure. Populations of bold three-spined sticklebacks (*Gasterosteus aculeatus*) had weaker ties between individuals in the social network, but a higher density of connections within this network, than did populations of shyer fish (Pike et al. 2008). However there is no clear pattern across species of whether personality types within a population shape social interactions, or whether social interactions shape the personalities of group members, and it is likely that the degree of heritability of a personality trait influences this causation. In three-spined sticklebacks individuals' personalities appeared to influence the dynamics of a social group (Laskowski and Bell 2014). However, colonies of social spiders (*Stegodyphus mimosarum*) that had higher familiarity among their members had more pronounced individual differences in boldness than colonies with low familiarity (Laskowski and Pruitt 2014), suggesting that individuals in groups with frequent interactions might adopt social niches that lead to the development of divergent personality types. The suggestion of social niches driving personality variation also seems to contrast with the evidence for homophily or social assortment based on temperament in some species of vertebrate. Stronger associations or network ties between individuals of similar personality types than between individuals with different personality types has been reported for the traits of boldness (Croft et al. 2009; Massen and Koski 2013; Carter et al. 2015), and exploratory tendency (Aplin et al. 2013) in wild populations. Social network analysis has revealed that individuals can also assort based on their level of sociability, where highly sociable animals are connected to other highly sociable animals (Croft et al. 2005; Wiszniewski et al. 2010; Best et al. 2015).

Personality can relate to multiple aspects of individuals' sociability. In various species, shyer individuals have been reported as having a lower propensity to leave foraging groups (Michelana et al. 2009), higher tendency to aggregate (Ward et al. 2004), and a greater number of connections with conspecifics (Pike et al. 2008; but see Croft et al. 2009). Individual body condition can modulate relationship between boldness and sociability (Öst et al. 2015), so it is likely that the relationship between boldness and sociability depends on multiple interacting environmental and intrinsic variables as well as the aspect of sociability being studied. Recently, the relationships between boldness and measures of sociability have been described in a wild mammal, the eastern

grey kangaroo (*Macropus giganteus*) (Best et al. 2015). In this species, boldness influenced individual kangaroos' trade-offs between foraging and vigilance (Edwards et al. 2013), and components of sociability related to females kangaroos' reproductive success (this thesis, Chapter 5), so both boldness and sociability are both likely to represent ecologically significant behaviours. Best et al. (2015) found that bolder female kangaroos tended to forage in smaller groups than did shyer individuals, and bolder females formed preferential associations with a greater proportion of their associates than did shyer females. This relationship between boldness and two different measures of sociability suggests that a boldness-sociability behavioural syndrome may exist in this species. However, it is not known whether the relationship between these two axes of personality is consistent over time, or under different environmental conditions. Eastern grey kangaroos graze in groups that regularly change in size and membership (Southwell 1984b), exhibiting 'higher fission-fusion dynamics' (Aureli et al. 2008) in their social organisation. Among species with this kind of sociality, there is little known about whether individuals associate based on similarity in temperament. Space use overlap (and to a lesser extent, genetic relatedness) contributes towards association patterns among female kangaroos (Best et al. 2014), but the contribution of similarity in personality measures to females' social relationships has not yet been investigated.

Our study builds on the work by Best et al. (2015) to further explore the relationship between boldness and social tendencies using the eastern grey kangaroo as a model species. Eastern grey kangaroos are gregarious, large-bodied grazing herbivores that forage in open-membership groups that vary in size and composition (Southwell 1984b). Although individuals frequently join and leave temporary sub-groups, non-random social organisation exists among females (Stuart-Dick 1987; Jarman 1994; Best et al. 2013). The population of eastern grey kangaroos that is the subject of the current study consists of approximately 300 animals that regularly forage at a national park in southeast Queensland, Australia. This population provides an ideal model in which to explore relationships between boldness and sociability in a wild mammal, in a study involving minimal disturbance to the natural social organisation and only minor disturbance to the animals tested. We collected four years of data on behavioural types and social organisation in the population to address the following aims.

First, we tested whether females were consistent in their boldness as measured by flight initiation distance (FID), and in multiple measures of sociability, over an extended time period with variability in environmental conditions. We focused on two measures that we hypothesised to represent different aspects of social behaviour. The first measure was the average sized group in which a female foraged, which represented a female's propensity to group with conspecifics in

general. The second measure was the number of preferred associates a female had (when controlling for individual gregariousness and space use overlap), which represented the strengths of her relationships with particular other individuals. Second, we tested whether the relationship between boldness and sociability, in which shyer females foraged in larger groups and formed preferred associations with a smaller proportion of their associates (Best et al. 2015), remained consistent over time. If individuals' levels of boldness and sociability remained consistent, we predicted that the overall relationship between these traits would also be consistent at the population level. Although we know that females in our population form persistent, non-random associations with one another, and some pairs of females associate more frequently than expected given their space use overlap, the factors that influence the strengths and existence of these associations are not well understood. Spatial overlap better explains pairwise associations than does genetic relatedness, yet it is unclear why some females preferentially associate more than expected based on their spatial overlap. Therefore, our third aim was to investigate whether the similarity in boldness between a pair of females related to their association strength, and to the preferential relationship status, among pairs of females. We hypothesised that females who were more similar in boldness would have higher association indices and be more likely to be preferred associates.

Methods

Field site and study population

Fieldwork was conducted at Sundown National Park (28°55'03''S, 151°34'46''E) in Queensland, Australia, at a 37.4-hectare field site inhabited by a population of eastern grey kangaroos (referred to as 'kangaroos' hereafter). The study area contains a mixture of grassland and open eucalypt forest habitats, and is used by approximately 230 female kangaroos and a smaller number of adult and sub-adult male kangaroos. Researchers have observed the population since 2009, and the kangaroos have become habituated to the presence of researchers to the extent that they can be approached to within 10 m for identification and collection of data without this affecting their behaviour. Animals were individually identified based on their natural features and markings (Jarman et al. 1989; Carter et al. 2009; Best et al. 2013). Identities of individuals were confirmed by referring to an extensive database of photographs, and by the use of genetic markers for a sub-set of individuals (described briefly in Chapter 4 of this thesis, and in detail by Best et al. 2013). All data collection for this study took place over 10 - 14 consecutive days each month from January 2010 until December 2013.

Association surveys

Social association survey data were collected following the method of Best et al. (2013). In brief, surveys were conducted once a day during the two-hour period after sunrise or before sunset until October 2012, after which they were conducted twice a day when conditions permitted. Kangaroos often changed groups during survey periods, and during the days would rest at the edges of the forest before forming new foraging groups in the evening, hence two surveys within a day were considered independent (Carter et al. 2009). In each survey, the researcher walked through the entire study area and recorded the identity of all adult and sub-adult females in each temporary foraging group of kangaroos that was encountered. A GPS location was also recorded close to the centre of each group using a Garmin eTrex H GPS (Garmin International Inc., Olathe, KS, U.S.A.) or close to the approximate location of each individual within the group when members were widely dispersed. Groups were defined using the 15-metre chain rule, in which individuals needed to be within 15 m of another group member to be considered part of the group (Jarman 1987). As per the gambit-of-the-group method, all members of a group were considered to be associating (Whitehead and Dufault 1999). Between January 2010 and August 2012, additional GPS locations for individuals were recorded opportunistically when they were encountered in the field during non-survey sessions. A female's reproductive state was recorded every time she was encountered, and female body condition index (BCI) was recorded once a month. BCI was based on a modified version of the index described by Best et al. (2015), with a kangaroo scored based on a visual estimate of the fat and muscle on her hips and ribs, and included categories 1 (poor), 2 (average), and 3 (good). Categories 3 and 4 from Best et al. (2015) were combined in the current study, since it was rare to encounter a female in category 4. Reproductive state was determined visually by the presence and size of a female's young. Females were classed as having NPY (no visible pouch-young), a SPY (small pouch-young - seen as a swelling in the pouch but not visible outside the pouch), a MPY (medium pouch-young - may have head or limbs projecting from the pouch), a LPY (large pouch-young - no longer fits completely into the pouch and may leave the pouch for short periods), or a YAF (young-at-foot - permanently excluded from the pouch but continues to nurse and remain close to its mother). Females could also have both a young-at-foot and a small pouch-young (SPY, YAF). Individuals not known to have bred were classed as sub-adult females (SF).

Quantifying Sociability

Association survey data were split into consecutive two-year time periods, 2010 - 2011 and 2012 - 2013, consistent with the periods over which FID tests were conducted. From these data, three types of measures of sociability were calculated for each individual in each time period (as described by Best et al. (2015) and briefly below) - mean group size (including only female group members),

social network metrics, and number of preferred associates. First, for females observed more than ten times during association surveys in a two-year time period (2010 - 2011 N = 171; 2012 – 2013 N = 177) we determined the mean foraging group size in which they were encountered. An estimate of individual consistency in foraging group size, using a method based on the intra-class correlation (ICC) test (Lessells and Boag 1987), was then calculated. A linear mixed effects model was conducted in R, using group size as the response variable, reproductive state as a fixed effect, and female ID and month as random effects. The variation in group size explained by between-individual effects was then determined from the model summary, and Markov Chain Monte Carlo (MCMC) sampling was used to estimate the within-individual variance for each female. A repeatability score for each individual that expressed the proportion of variance in their group size attributable to between-individual effects was then generated, with scores closer to one representing higher repeatability.

To calculate individuals' social network metrics, association survey data from each two-year time period were entered into the program SOCPROG2.4 (Whitehead 2009) to generate a matrix of association indices among all females. The association index used was the half-weight index (HWI), a commonly-used association index given by the formula HWI = $N_{ab}/0.5(N_a/N_b)$, where N_{ab} is the number of sampling periods where individuals A and B were observed associating, N_a is the number of sampling periods where A was observed, and N_b is the number of sampling periods where B was observed (Cairns and Schwager 1987). HWI values were then transformed to control for individual differences in gregariousness (Godde et al. 2013), generating a pairwise association measure known as the HWIG. From these association matrices of HWIG values, we used SOCPROG2.4 to calculate social network metrics for individuals. Scores were generated for the social network metrics of strength (the sum of an individual's association indices with all other individuals it is connected to in the network), clustering coefficient (the degree to which an individual's associates are connected amongst themselves in the network), and affinity (the weighted average strength of an individual's neighbours in the network) (Whitehead 2008).

To quantify a third aspect of individuals' sociability, we controlled for pairwise space use overlap to determine which pairs of females associated more frequently than expected (Best et al. 2014). In each two-year time period, social association survey and GPS data for females that had been recorded on surveys more than ten times, and for whom we had 50 or more GPS locations, were entered into the R package Digiroo2 (Dwyer et al. 2013). Digiroo2 created null models for associations by generating simulated HWIG association indices based solely on spatial overlap between individuals. Two hundred simulated sets of HWIGs involving all individuals were created

and then compared to the observed HWIGs. Pairs of females with observed HWIGs in the top 2.5% of their simulated HWIGs were termed 'preferred associates', pairs with observed HWIGs in the bottom 2.5% were said to avoid each other, and all pairs with HWIGs falling within these limits were classed as 'casual associates'. The measure of individual sociability derived from this analysis was the number of preferred associates each female had in each time period.

Testing boldness using flight initiation distance

As described by Best et al. (2015), 51 female kangaroos were tested multiple times in flight initiation distance trials during an 18-month period in 2010 and 2011. These females were known to have bred for the first time prior to or during 2010. Additional FID trials were conducted on 58 female kangaroos, following the method of Best et al. (2015), over two months (May and June) in 2012 and from February to December 2013. Thirty-six of these females had been previously tested in 2010 - 2011, and these were classed as 'older' females. The remaining 22 females were born in 2009 or 2010 and were approaching reproductive maturity when FID testing began, and were classed as 'younger' females. To conduct the FID trials the researcher and an assistant (with whom the kangaroos were unfamiliar) walked through the study site until a target female kangaroo was encountered and identified. The assistant then positioned themself facing the female kangaroo front on, ten meters away, and remained there until the target female and all members of her foraging group had lowered their heads to resume grazing. Once this had occurred, the assistant walked towards the target female at a brisk pace (~6 km/hr) and continued their approach until the kangaroo moved both its feet and moved away. The distance between where the kangaroo had been standing and where the assistant stopped was then measured with a 30 m measuring tape, and this was recorded as the animal's FID. The number of female group members in the group in which the individual was tested in was also recorded, as was the wind speed at the time of the testing, using a Kestrel® 1000 Pocket Wind Meter (Nielson-Kellerman Co., Boothwyn, PA, U.S.A). Each individual was tested between six and thirteen times over the period of data collection.

Quantifying boldness

Methods and results for FID tests conducted in 2010 - 2011 have been published previously (Best et al. 2015). To determine whether there were also significant between-individual differences and within-individual consistency in FID scores in 2012 - 2013, a linear mixed effects model fit by restricted maximum likelihood (REML) was conducted in R (R Core Team 2013) using the package 'lmerTest' (Kuznetsova et al. 2014). The response variable was FID in metres, and explanatory variables were females' BCI, females' reproductive state, the number of prior FID tests conducted on the female during 2012 - 2013, the size of the group the female was tested in, wind speed, the

time of day females were tested (morning or evening), and female age class ('older' or 'younger'). Female kangaroo ID and the identity of the field assistant used to conduct the test were included as random effects. ANOVA tests were run on versions of the model with each random effect removed in turn to assess the significance of the effects in the model. We then calculated the individual repeatability of FID based on the full model, using the method described above.

Long-term consistency of sociability

To test the consistency of females' measures of sociability over an extended time period, we performed Pearson product-moment correlations for two measures of sociability, mean group size and number of preferred associates, comparing results from 2010 - 2011 and 2012 - 2013. We included individuals present during both time periods and for whom we had more than ten observations on social association surveys and at least 50 GPS positions recorded during each period (N = 77).

Long-term consistency of boldness

To test whether individual differences and intra-individual consistency in FID persisted over four years, FID measures from 36 females that were tested in both 2010 - 2011 and 2012 - 2013 were included in a linear mixed effects model fit by REML using the package 'lmerTest'. FID in metres was the response variable, and explanatory variables used were wind speed, group size the female was tested in, female BCI, female reproductive state, total number of times the female had been tested in both years, session time, and period of testing (2010 - 2011 or 2012 - 2013). Female ID and field assistant identity were included as random effects. Individual consistency in FID was calculated using the random effect from the full model, as described above. To compare an individual's boldness between time periods, individuals' mean FID scores in each period were correlated using a Pearson product moment correlation.

Relationships between boldness and sociability measures

We investigated the relationships between individuals' mean FID scores and their mean foraging group size, number of preferred associates, strength, clustering coefficient, and affinity, using Pearson product-moment correlations, for females that were tested for FID and for whom we had recorded at least 50 GPS locations in 2012 - 2013 (N = 57). All of the above measures were calculated with data from the 2012 - 2013 time period.

Testing for social assortment based on boldness

To determine if females assorted into foraging groups based on similarity in boldness, we took the absolute difference in mean FID scores between each pair of females in each time period to represent a measure of similarity in boldness, where pairwise values closer to zero indicated that the two individuals were more similar in this behavioural trait. These values were then entered into a symmetric matrix. For the same pairs of females in each time period, we took their pairwise HWIG association indices and created a second symmetric matrix. This allowed us to look at dyadic associations among a subset of females while considering their gregariousness in the context of the larger population. For 2010 - 2011 these matrices included all 51 females tested for FID, while in 2012 - 2013 they included 57 of the 58 females tested for FID. For each time period, the HWIG matrix and the matrix of pairwise differences in average FIDs were tested for similarity using a Procrustean superimposition method (Peres-Neto and Jackson 2001). This test assesses the overall degree of association between two matrices by scaling and rotating matrices of raw data, rather than measuring associations between distance matrices like the more common Mantel test. The Procrustes test is equally as or more powerful than the Mantel test, particularly when the matrices have an intermediate degree of association (Peres-Neto and Jackson 2001). We conducted the Procrustes test with 999 permutations, using the function 'protest' in the R package 'vegan' (Oskanen et al. 2013). In this test, a significance value of less than 0.05 means that the null hypothesis – that the matrices have a correlation of zero – can be rejected. Because we included 'younger' aged females in the 2012 - 2013 analysis but not in the 2010 - 2011 analysis, we suspected this could confound the results. To control for this influence, we repeated the Procrustes superimposition tests using truncated versions of each matrix that included only the 36 females tested for FID during both 2010 - 2011 and 2012 - 2013.

To determine if females' preferential associations were based on similarity in boldness, we repeated the Procrustean superimposition tests described above, but replaced the HWIG matrix with a binary matrix indicating whether each pair of females were preferred associates or not. This matrix was then tested for its similarity to the matrix of mean FID differences in both time periods.

Results

Consistency of individual differences in temperament

Boldness

In 2012 - 2013, 58 females were tested for FID on between six and thirteen occasions (mean number of tests = 11.2 ± 1.6). Females' mean FIDs tended to be shorter in 2012 - 2013 than in 2010

- 2011 (mean of all females' mean FIDs: 2010 - 2011 = 4.08 m ± 0.80, range of individuals' mean FIDs = 2.68 – 6.94 m); 2012 – 2013 = 3.59 m ± 0.65, range of individuals' means FIDs = 2.36 – 5.66 m) (Figure 1). Within each two-year time period, females differed significantly in their FIDs. Best et al. (2015) previously reported that within-individual consistency in FID was high and between-individual differences in FID were significant; here, we report the findings from 2012 - 2013. Individual ID explained 22.0% of the variation in FIDs, and was significant when dropped from the full model (X^2 = 72.28, df= 1, $p < 0.0001$). Intra-individual consistency of FID was high, with mean intra-class coefficients (ICCs) of 0.798 (range 0.693 – 0.857, N = 58 females). Several model parameters were significantly related to females' FIDs, including reproductive state, time of day, and the identity of the assistant used to conduct the test (Supplementary Material). However, there was no significant influence of wind speed, female age class, female body condition index, number of previous FID tests performed on a female, or the size of the group a female was tested in (Supplementary Material).

When a linear mixed effect model was run that included FID measures from the females tested during both 2010 - 2011 and 2012 - 2013 (N = 36), individual ID as a random effect was significant (X^2 = 123.12, df= 1, $p < 0.0001$) and explained 19.8% of the variance in FID. High within-individual consistency of FID measures was found in this model (mean ICC = 0.865, range 0.791 - 0.889). FID was not significantly related to the time period in which a test was conducted, the time of day of the test, wind speed, females' BCIs, or females' reproductive states. However, numbers of tests conducted previously on females, and the sizes of the groups they were tested in, were significant in the model (Supplementary Material). Individuals' mean FIDs in 2010 - 2011 were highly correlated with their mean FIDs in 2012 - 2013 (Pearson product-moment correlation, r = 0.714, $p < 0.0001$).

Sociability

Consistent individual differences in foraging group size for individuals in 2010 - 2011 were reported by Best et al. (2015). In 2012 - 2013, females were highly consistent in the sizes of the groups they foraged in (N = 177 females, mean ICC = 0.759, range 0.593 - 0.884), based on the intra-class correlation coefficient, which was determined from a linear mixed effects model with reproductive state as a fixed effect and female ID and month as random effects. For females observed on surveys more than ten times and for whom we had at least 50 GPS locations recorded in each two-year time period (N = 77), the mean foraging group size in which an individual was encountered in 2010 - 2011 was significantly positively correlated with the mean group size in which she was encountered in 2012 - 2013 (Pearson's product-moment correlation, r = 0.336, p =

0.003) (Fig. 2a). Another measure of sociability, the number of preferred associates an individual had, was also significantly positively correlated between 2010 - 2011 and 2012 - 2013 (Pearson's product-moment correlation, $r = 0.796$, $p < 0.0001$) (Fig. 2b).

Relationships between boldness and sociability measures

In 2012 – 2013, females' mean FIDs were significantly positively correlated with the mean foraging group size in which they were encountered (Pearson's product-moment correlation, $r = 0.319$, $p = 0.020$) (Figure 3a). There was a trend for females' mean FIDs to correlate negatively with their numbers of preferred associates, although this did not reach significance ($r = -0.213$, $p = 0.127$) (Figure 3b). Individuals' mean FIDs were not significantly correlated with any of three social network measures from 2012 - 2013, although the relationships between FID and clustering coefficient, and FID and affinity, approached significance (strength, $r = -0.224$, $p = 0.094$; clustering coefficient, $r = -0.246$, $p = 0.065$; affinity, $r = -0.243$, $p = 0.068$).

Social assortment based on boldness

Pairwise association strength did not consistently relate to pairwise similarity in boldness in the two time periods. In 2010 - 2011 there was a modest significant positive correlation between the HWIG association matrix and the mean FID difference matrix ($N = 51$, $r = 0.304$, Procrustes Sum of Squares = 0.908, $p = 0.033$). In 2012 - 2013 this correlation was weaker, and was not significant enough to reject the null hypothesis that the two matrices had zero similarity ($N = 57$, $r = 0.267$, Procrustes Sum of Squares = 0.929, $p = 0.092$). When these analyses were repeated including only the 36 individuals present in both time periods, the correlation between FID similarity and association index remained positive and significant in 2010 - 2011 ($N = 36$, $r = 0.371$, Procrustes Sum of Squares = 0.862, $p = 0.021$), while the correlation between the matrices from 2012 – 2013 remained non-significant ($N = 36$, $r = 0.246$, Procrustes Sum of Squares= 0.940, $p = 0.332$). Pairwise differences in mean FID scores were not related to pairwise preferential associate status in either 2010 - 2011 ($N = 51$, $r = 0.255$, Procrustes Sum of Squares = 0.935, $p = 0.293$) or 2012 - 2013 ($N = 57$, $r = 0.251$, Procrustes Sum of Squares = 0.937, $p = 0.250$).

Discussion

We have demonstrated that individual female kangaroos are consistent in their measures of boldness and of sociability over multiple years, a longer time period than has been previously tested in this species. The relationship between boldness and foraging group size in the population

persisted over two two-year time periods, whereby shyer females foraged in larger groups. The tendency for shyer individuals to have fewer preferred associates, as reported previously by Best et al. (2015) for females in 2010 - 2011, was not found to be significant in 2012 - 2013, although the results showed a trend towards this pattern. Female kangaroos showed a modest and significant degree of social assortment by boldness, where individuals that were more similar in mean FID scores had higher pairwise HWIG association indices, but this pattern of social assortment did not persist between testing periods and did not appear to contribute towards preferential pairwise associations.

Long-term consistency of personality traits, and their correlations

We found significant between-individual differences and within-individual consistency in boldness, as measured by FID, over a four-year period. Few studies have tested personality dimensions of wild mammals in their natural environment over such a long time period, although female bighorn sheep were tested in the field for trappability (representing boldness) and docility over a period of four years by Réale et al. (2000). Although several explanatory variables were significantly related to FID in each time period in the linear mixed effects models, individual ID explained equivalent amounts of variation in FID, and was a significant parameter, in both two-year time periods. Individual ID explained slightly less variation in FID scores over a four-year period, but since behaviour has generally been found to be more repeatable when tested over shorter rather than longer time periods (Bell et al. 2009), was not unexpected. As shown by the intra-class correlation coefficient tests, the degree of individual consistency in FID was also very similar between these time periods. There are concerns that using the ICC method does not consider changes in a trait over time, and can therefore overestimate the broad-sense repeatability of a trait (Biro and Stamps 2015). However, given our large sample sizes and that our generalised linear mixed models considered observation number (i.e. number of previous tests), we feel that temporal change was adequately controlled for. We were therefore confident in using an individual's average FID score in subsequent analyses as a highly consistent index of boldness. It should be noted, however, that multiple factors are likely to affect individuals' FIDs, and some of these were significant predictors in the linear mixed effects models. The use of more advanced statistical techniques should be considered in future to control for the influence of these such variables on mean FIDs.

We chose to focus on a number of different measures of sociability: mean foraging group size, number of preferred associates, and social network analysis measures. The first two measures

appear to represent different facets of sociability, and it would be interesting to see how these measures relate to each other and whether they relate consistently this way between time periods. Sociability can be quantified in several ways, even within the same species (e.g. Croft et al. 2009), yet due to a lack consistency in terminology in the field it is unclear whether these measures might represent the same underlying trait or different personality traits (Koski 2014). We found that the average sized group in which a female was encountered was moderately yet significantly correlated between time periods, and showed a high degree of individual consistency over time. However, in addition to personality traits, environmental variables are likely to help shape individuals' grouping behaviour. Predator presence can influence group sizes in eastern grey kangaroos (Banks 2001), and individuals' preferred group sizes may reflect how they balance the perceived risk of predation with the costs of grouping, which can include increased feeding competition and higher risk of parasite or disease transmission (Krause and Ruxton 2002) . Population density can also influence sizes of kangaroo groups (Southwell 1984a). It is also possible that the composition of the population may have influenced foraging group sizes. There were a greater number of sub-adult females in the population during 2012 - 2013 after a large proportion of young survived post-weaning due to favourable conditions in 2011 (Best et al. 2015). In another mammal with high fission-fusion dynamics, northern long-eared bats (*Myotis septentrionalis*), females of all age classes roosted most frequently with younger individuals, and it was suggested that younger females may be more socially exploratory and may play a role in maintaining group-wide social connections (Patriquin et al. 2010). If younger females have similar social roles in our study population of kangaroos, then population age structure may influence group-wide social structure.

We have shown that the correlation between boldness and mean group size persisted between time periods, fitting the criteria for a behavioural syndrome (Sih et al. 2004) involving boldness and this measure of sociability. The consistent relationship between these behavioural measures reported both here and by Best et al. (2015) is similar to findings in some other species. Shyer three-spined sticklebacks had a greater tendency to shoal (Ward et al. 2004), a behaviour thought to represent a tradeoff between resource gains and predation risk. Similarly, bolder sheep were more likely than shyer sheep to split from a foraging group as its number of members increased (which represented increased feeding competition at a patch) (Michelana et al. 2009). However, in contrast to Best et al. (2015) who reported that bolder females formed preferential associations with fewer of their associates, we did not find that boldness was significantly inversely correlated with females' number of preferred associates during 2012 - 2013. Despite the fact that females' numbers of preferred associates was highly correlated between time periods, it is possible that the measure of number of preferred associates (used in the current study) did not accurately reflect the proportion

of an individual's associates that were preferred (used by Best et al. 2015), which may explain the result obtained. Repeating the current analysis using the latter measure of females' social preferences would allow the persistence of the boldness and sociability behavioural syndrome to be investigated in greater detail.

Of the 58 kangaroos tested for FID during 2012 - 2013, 36 females had been known to reproduce during the previous two years (categorised as 'older' females), and 22 were sub-adult females that were to reach breeding age during 2012 - 2013 ('younger' females). We found no significant influence of female age on FID when controlling for other variables in the model. Similarly, Réale et al. (2000) found that boldness and docility did not relate to age in wild bighorn ewes, although experimentally assessed boldness scored tended to decline with age in captive female chimpanzees (*Pan troglodytes*) (Massen et al. 2013). Given that we have multiple measures of sociability for females that were present in both time periods and who were sub-adults during 2010 - 2011, future analyses could test whether repeatability of sociability traits was different for older and younger females. Juveniles may be more plastic in their personalities, as shown in yellow-bellied marmots (*Marmota flaviventris*) where juveniles were less repeatable in their boldness (as measured in the field by FID) than were yearlings (Petelle et al. 2013). Further work could examine this consistency between age classes, to understand more about the development of personality.

Social assortment by boldness

Females showed moderate social assortment by bold temperament in 2010 - 2011, but not in 2012 - 2013, and these patterns remained the same when only the associations among the same 36 females were considered in each time period. The lack of consistency of social assortment by boldness between these time periods, even when attempting to control for changes in population demographics, may have been due to the large number of female young weaned between June 2011 and June 2012 by females tested for boldness. Eastern grey kangaroo mothers can maintain close post-weaning associations with their female offspring (Stuart-Dick 1987; Jarman 1994), which tend to be strongest during the first year post-weaning (C. Menz, unpublished data). The presence of sub-adult daughters (or of other female relatives) in the population may be stronger drivers of pairwise associations than similarity in temperament, and this could be addressed in future work.

In species with higher fission-fusion social systems, association rates can correlate strongly with spatial proximity or overlap of space use, although this relationship is not always considered (but see Chaverri et al. 2007; Frère et al. 2010; Carter et al. 2013; Wakefield 2013). Therefore, in addition to using the HWI to represent dyadic association strength, we tested for social assortment by boldness using a binary measure of pairwise associations that controlled for individual gregariousness and for space use overlap: preferential association status (Carter et al. 2009; Best et al. 2014). We found that there was no relationship between pairs' preferential association status and the difference in their mean FID scores. This suggests that similarity in boldness does not influence females' choice of whom they go out of their way to associate with (or, alternatively, a pair that associate preferentially do not develop similar personalities). In a recent review of personalities in a social network context, Krause et al. (2010) cautioned that spatial overlap should be considered when measuring social assortment, to control for the fact that individuals of similar personalities may associate because they have mutual attraction for the same habitat or area. Individuals similar in boldness may share similar habitat preferences, and the distribution of different personality types within a site according to these preferences could influence who individuals come into contact with, as suggested by Croft et al. (2009). There is some evidence that individuals within a population with different personalities utilise their habitats in different ways, (Wilson et al. 1993; Boon et al. 2008; Hensley et al. 2012), possibly reflecting trade-offs between foraging success and risk of predation, and this could be investigated in future work on eastern grey kangaroos. The specific habitat use of females was not looked at in this study, since all data were collected in similar open grassy habitats. However, future research could perhaps incorporate additional vegetation coverage data into individuals' space use measures, to see whether this variable influences grouping patterns or boldness. Given that biparental genetic relatedness is a weak predictor of preferential associations (Best et al. 2014, and this thesis, Chapter 3), and it is likely that similarity in boldness does not explain these social preferences either, the factors contributing to preferential associations among females are still not fully known, and should be investigated further.

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Figure legends

Figure 1. Lineplot comparison of mean flight initiation distance (FID) measures (y-axis) for 36 individual female kangaroos (represented by black circles) in both 2010 - 2011 and 2012 - 2013. Individuals' means in each time period are connected by lines.

Figure 2. Consistency of two measures of sociability for 77 individual female kangaroos in 2010 - 2011 and 2012 - 2013, for (a) mean foraging group sizes, and (b) numbers of preferred associates.

Figure 3. Relationships between measures of boldness and sociability in 2012 - 2013 in 57 female kangaroos, for (a) mean foraging group size and mean FID, and (b) number of preferred associates and mean FID.

Figures

Figure 1

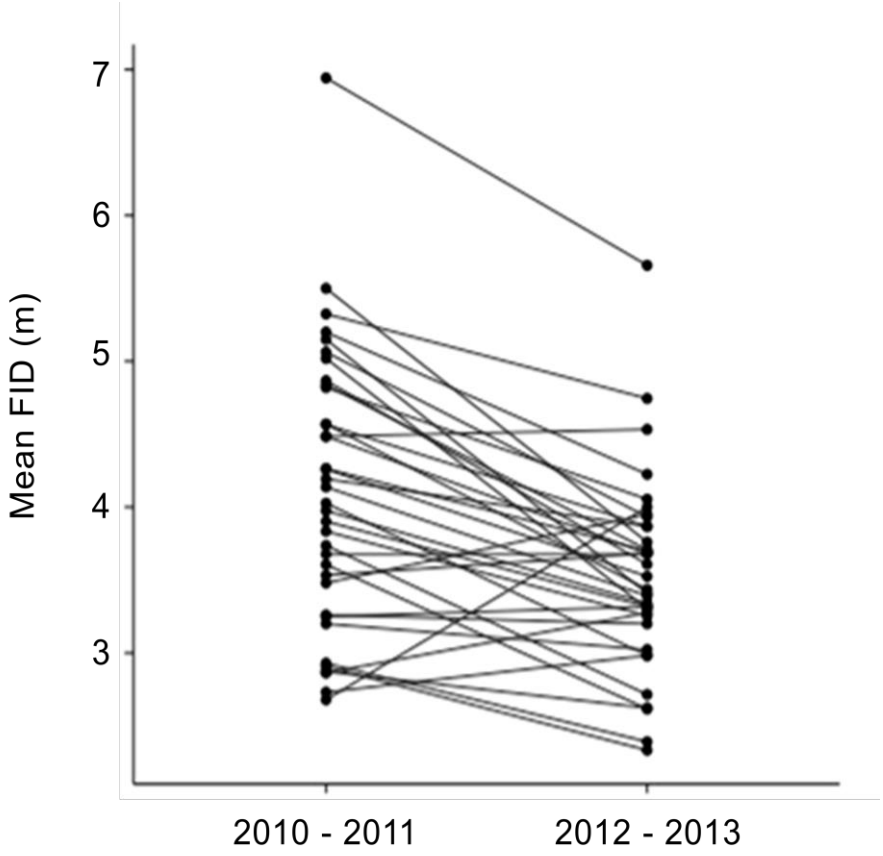


Figure 2

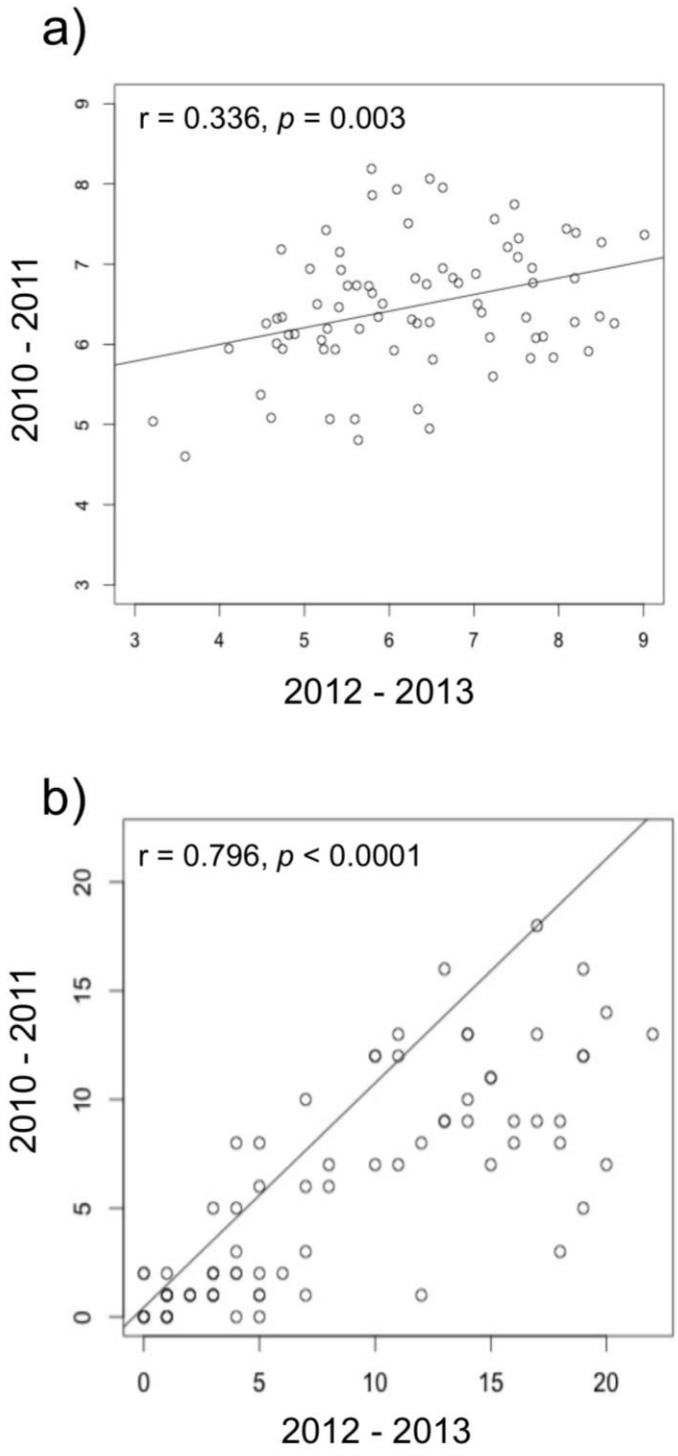
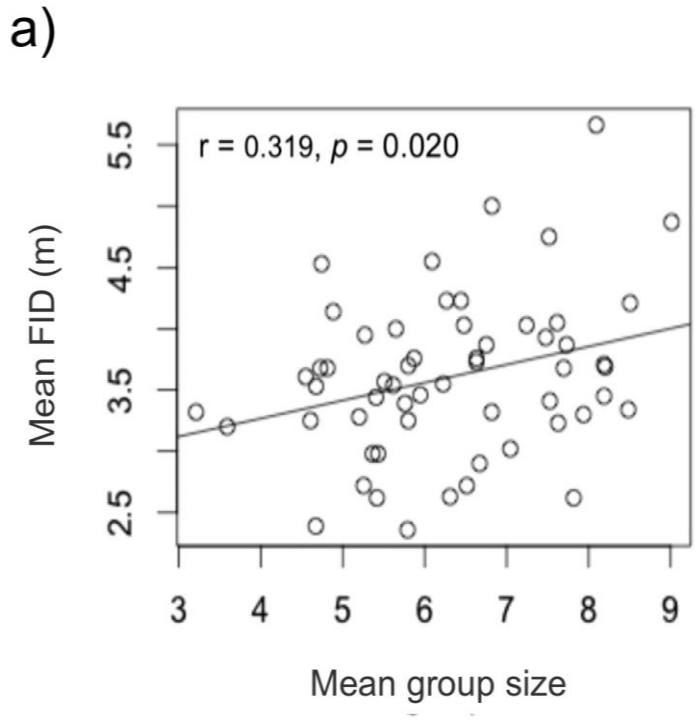
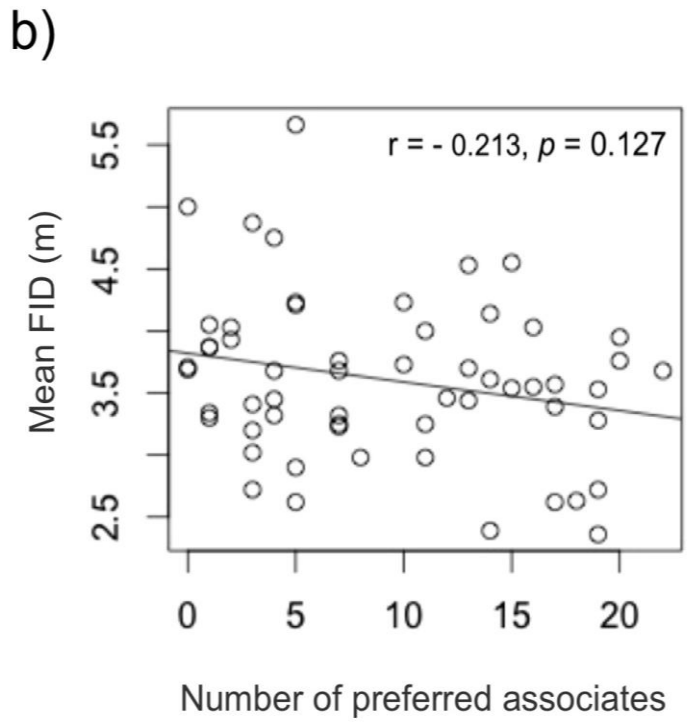

a)
r = 0.336, p = 0.003
2010 - 2011
2012 - 2013
b)
r = 0.796, p < 0.0001
2010 - 2011
2012 - 2013

Figure 3


a)
r = 0.319, p = 0.020
Mean FID (m)
2.5
3.5
4.5
5.5
3
4
5
6
7
8
9
Mean group size


b)
r = - 0.213, p = 0.127
Mean FID (m)
2.5
3.5
4.5
5.5
0
5
10
15
20
Number of preferred associates

Supplementary Material

Significant parameters in linear mixed effects models of factors affecting FID

In 2010 - 2011, several model parameters were significant contributors to FID in female kangaroos; these have been previously reported (Best et al. 2015). To summarise, females tested in smaller groups, and those tested at higher wind speeds, had larger FIDs. Reproductive state, the identity of the assistant used to conduct the tests, and the number of tests previously conducted on an individual also significantly affected FID. In 2012 - 2013, a linear mixed effects model fit by REML was used to determine the variables influencing FID for 58 individual females. An ANOVA test using the Satterthwaite approximation for degrees of freedom was performed to assess the significance of the model fixed effects. There were no significant effects on FID of age class ($F_{1, 78.41} = 0.554$, $p = 0.459$), body condition index ($F_{2, 457} = 0.436$, $p = 0.647$), size of the group a female was tested in ($F_{1, 438.93} = 0.025$, $p = 0.875$), wind speed ($F_{1, 445.43} = 1.034$, $p = 0.310$), or number of previous FID tests performed in 2012-13 on that female ($F_{1, 50.98} = 3.430$, $p = 0.070$). Reproductive state was significant ($F_{6, 450.28} = 2.942$, $p = 0.008$), but with no clear trend for FID to vary in a linear fashion with the age/size of a female's dependent young. The time of day an individual was tested was significant ($F_{1, 443.52} = 6.379$, $p = 0.012$), with females tested in the afternoon having significantly longer FIDs. The full model was compared to a version in which the random effect of field assistant identity was excluded, and assistant identity was found to be significant ($X^2 = 36.98$, df= 1, $p < 0.001$).

A second linear mixed effects model was run for the FID measures of the 36 females tested in both the 2010 – 2011 and 2012 – 2013 time periods. Females were tested an average of 24.6 ± 4.2 times (range 12 – 33) across both time periods. There were no significant effects on FID of female reproductive state ($F_{5, 755.44} = 1.016$, $p = 0.407$), body condition ($F_{2, 760.01} = 1.058$, $p = 0.348$), wind speed ($F_{1, 745.11} = 2.326$, $p = 0.128$), time of day ($F_{1, 733.38} = 1.100$. $p = 0.295$), or time period in which the female was tested ($F_{1, 24.72} = 0.077$, $p = 0.784$). Females tested in smaller groups had significantly longer FIDs ($F_{1, 734.88} = 4.673$, $p = 0.031$), although the inter-quartile range of the average group sizes that each female was tested in was small (1st Quartile = 4.16, 3rd Quartile= 5.84). FID was significantly related to the tests performed on a female ($F_{1, 114.47} = 14.111$, $p < 0.001$) and decreased with greater numbers of tests, as was reported by Best et al. (2015), who found that habituation to the FID test was strongest during the first five tests on a given female. Finally, assistant ID (N = 15) was also a significant random effect when dropped from the model in an ANOVA ($X^2 = 85.24$, df= 1, $p < 0.0001$).

How important is relatedness in structuring female kangaroos' patterns of association?

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Abstract

Female-biased natal philopatry is a common occurrence among group-living mammals, with relationships among multiple generations of females forming the basis of social structure in many species. In species that exhibit higher fission-fusion dynamics in their grouping patterns, the strengths of social relationships or associations among females can often be explained by genetic relatedness. Spatial overlap often also contributes to associations, but few studies have examined the relative contributions of kinship and space use in explaining association patterns. In the eastern grey kangaroo (*Macropus giganteus*), a gregarious herbivore with higher fission-fusion grouping dynamics, close post-weaning associations between mothers and their female offspring have been described, but population-wide genetic structure based on biparental relatedness tends to be weak. However, the influences of the social relationships of sub-adults on association patterns have not been explored in detail. In this study, we use four years of social association data from a wild population of individually identified eastern grey kangaroos to investigate the degree to which pairwise associations are related to kinship (both biparental and maternal), and the extent to which inclusion of sub-adults in the analysis influences this relationship. We used microsatellite genotyping data from approximately 200 females to estimate biparental relatedness measures, and mitochondrial DNA and observational pedigrees to identify mothers and daughters within the population. Across all four years the correlations between biparental relatedness and association strengths were weakly yet significantly positive, both when including and excluding sub-adults from the analyses, although these correlations weakened when controlling for pairwise space use overlap. The mother-daughter status of pairs explained a greater proportion of the variation in association strengths than did biparental relatedness estimates, even among adult females, and mother-daughter pairs were more likely than not to form preferential associations. Our findings suggest that even though some females continue to associate closely with their adult daughters, this kind of subtle pattern can be masked when only biparental kinship measures are considered.

Introduction

Living with kin forms the basis of sociality for many vertebrate species (Clutton-Brock 2002). When offspring continue to share space or associate with their parents after maternal care ends, kin structure can develop within a population. Sex-biased dispersal is common in mammals, and females are usually philopatric, remaining to breed in their natal group or range, while males often disperse from their natal group (Greenwood 1980; Clutton-Brock and Lukas 2012). Such male-biased dispersal can lead to social units in a group being based around maternal relatives. Kin selection is predicted to evolve when animals are able to obtain inclusive fitness benefits from helping their relatives (Hamilton 1964), and there is strong evidence for kin selection among at least some cooperatively breeding mammals (Clutton-Brock 2002; Smith 2014). In many gregarious species that do not breed cooperatively, philopatric individuals often live near their close relatives, and this fine-scale genetic structure across a population can provide opportunity for kin selection to operate in the absence of cooperative breeding (reviewed by Hatchwell 2010). Animals can favour kin not only through cooperative breeding, but also through other forms of social behaviours such as choice of social partners, coalition formation, and social tolerance (Smith 2014).

The ability to identify closely related individuals is a necessary precursor for individuals to bias social behaviour towards kin (Holmes and Sherman 1983). Kin discrimination abilities vary among species, with the strongest discrimination occurring when the benefits of nepotism are greatest (Griffin and West 2003). Two common mechanisms are thought to facilitate kin discrimination in mammals: familiarity and phenotype matching. Familiarity can develop from close associations with relatives, such as parents or littermates/siblings, during a critical developmental period (Tang Halpin 1991). Mother-offspring recognition is the most common example of this kind of kin recognition. Phenotype matching involves an individual using itself, or a known relative, as a template to identify others that have a similar phenotype (Holmes 1986). Olfactory cues are commonly used in phenotype matching among mammals, although appearance and vocalizations can also be used to identify kin (reviewed by Widdig 2007).

Phenotype matching can play a role in identification of paternal kin who otherwise might not be known to an individual through familiarity (Widdig 2007). Among mammals that live in multi-male multi-female groups, there is often high reproductive skew in males, with a small number of high-ranking individuals siring most offspring in a breeding period (Widdig 2013). This skew can create large cohorts of half-siblings in the population. In addition to preferentially associating and interacting with maternal relatives, primates have been found in some studies to recognize and

favour these paternal half-siblings over unrelated or distantly-related group-mates (Widdig et al. 2001; Smith et al. 2003; Schülke et al. 2013), although this has not always been the case (Langergraber et al. 2007; Perry et al. 2008; Weinstein and Capitanio 2008). The majority of research comparing the importance of maternal and paternal kinship in relationships among social mammals has been done with primates, although some studies have researched other mammals. In both spotted hyenas (*Crocuta crocuta*) and Belding's ground squirrels (*Spermophilus beldingi*), individuals showed differential behaviour towards paternal kin (which they would not recognize through familiarity) compared to non-kin (Holmes 1986; Wahaj et al. 2004).

In species with higher fission-fusion dynamics, individuals can freely join and leave sub-groups that can vary in size, composition and spatial cohesion (Aureli et al. 2008). In this type of social system, average pairwise association strengths across the population tend to be weak, but individuals nonetheless often show differentiated and non-random associations with conspecifics. Kinship often contributes to association patterns within a higher-fission fusion context, as reported in giraffe (*Giraffa camelopardis*) (Carter et al. 2013), bottlenose dolphins (*Tursiops* spp.) (Frère et al. 2010; Wiszniewski et al. 2010), and African elephants (*Loxodonta africana*) (Archie et al. 2006). This kin structure occurs both in species with complex cooperative behaviours and in those that do not exhibit cooperation. However, the degree of influence of kinship on association patterns varies from weak (e.g. giraffes, Carter et al. 2013) to strong (e.g. elephants, Archie et al. 2006), and relatedness sometimes does not explain association strengths at all, as in big brown bats (*Eptesicus fuscus*) (Metheny et al. 2008). In a number of social ungulate species with higher fission-fusion dynamics, including bison (*Bison bison*) (Green et al. 1989), wild boar (*Sus scrofa*) (Kaminski et al. 2005), red deer (*Cervus elaphus*) (Guinness et al. 1979) and giraffe (Bercovitch and Berry 2013), mothers continue to associate to some degree with their female offspring following weaning. These associations can persist when daughters reach adulthood in some species, for example mountain goats (*Oreamnos americamus*) (Godde et al. 2015). The separate influences of matrilineal and patrilineal relatedness on female association patterns in higher fission-fusion populations have not been extensively studied. However, in bottlenose dolphins matriline membership was more strongly correlated with association strengths than was biparental relatedness (Wiszniewski et al. 2010), and in a different population the relationship between association strengths and biparental relatedness varied depending on females' matriline memberships (Frère et al. 2010).

Eastern grey kangaroos (*Macropus giganteus*) are large-bodied members of the Macropodidae, a family of marsupials considered to be the ecological equivalents of ungulates (Jarman 1983). One of the most gregarious of the macropod species, eastern grey kangaroos forage in temporary groups

that frequently change in size and composition (Southwell 1984; Jarman and Coulson 1989), making them a species with higher fission-fusion dynamics in their social organization. Females tend to be philopatric, remaining in their natal areas to breed amongst their female relatives, and males often disperse (Zenger et al. 2003; Coghlan 2013; King et al. 2015b). Mothers often continue to associate to some degree with both their sons and daughters after they are weaned (Stuart-Dick 1987). Males exhibit a polygynous mating system based on a dominance hierarchy (Jarman 1983) and are not involved in parental care. Eastern grey kangaroos do not groom one another (except for mothers grooming offspring), care for others' young, or engage in other cooperative interactions, yet females can form non-random and persistent associations over time (Best et al. 2013). Although space use patterns explain some these social preferences to some degree, close associations between females can occur even when pairs have minimal overlap between their foraging ranges (Stuart-Dick 1987; Carter et al. 2009; Best et al. 2014), while other pairs that share a large proportion of their ranges may rarely or never associate. While it is still unclear why some pairs can have close social relationships in the absence of high space use overlap, pairwise genetic relatedness is likely to explain these patterns to some degree.

Based on long-term studies of different populations of eastern grey kangaroos, it is likely that the extent to which kinship influences females' association strengths varies with population density and demographics. In a low-density population of eastern grey kangaroos at Wallaby Creek in New South Wales, Jarman (1994) reported that females were likely to have a female relative as their closest associate. However, in his population only matrilineal relatedness was known (based on behavioural observations, since molecular techniques for analyses of relatedness were not yet available at the time of their study), so the contribution of paternal kin to association patterns within the population was not known. More recent studies in other populations of eastern grey kangaroos have used genetic markers to determine biparental relatedness estimates (i.e. those that consider both paternal and maternal genetic contributions) among individuals in the population, using microsatellite markers, and then explored how these relate to association patterns and space use. In a population at Sundown National Park in Queensland, pairwise association strengths were weakly ($r = 0.13$) yet significantly correlated with biparental genetic relatedness, and females were philopatric at a fine spatial scale (Best et al. 2013; Best et al. 2014). In addition, individuals clustered into spatially overlapping communities, with significantly higher association measures within than between communities and higher mean pairwise relatedness between individuals within a community (Best et al. 2013). However, this study did not differentiate between adults and sub-adults, making it possible that close post-weaning associations between mothers and their sub-adult daughters could have contributed significantly to these patterns. In a different population of higher

density than the other two mentioned, at Wilsons Promontory National Park in Victoria, positive yet weak fine-scale genetic structure was found among adult females, but such genetic structuring was suggested to reflect dispersal patterns in this high-density population rather than active associations among kin (King et al. 2015b).

Kangaroo mothers are thought to recognize their offspring through olfaction (Russell 1989), although a report of pouch-swapping and adoption of pouch-young in the Wilsons Promontory eastern-grey kangaroo population suggests that this mechanism of recognition may be weak, at least in the period soon after the young first emerges from the pouch (King et al. 2015a). Limited evidence exists of kin discrimination in macropods beyond mother-offspring relationships. However, female tammar wallabies (*Macropus eugenii*) in captivity had fewer aggressive interactions with kin than with non-kin when experimentally paired with animals with which they had no prior familiarity (Blumstein et al. 2002), suggesting that the observed kin discrimination is likely dependent on olfactory-based phenotype matching. Based on these observations, it is possible that macropods may be able to identify their relatives not only through familiarity but also through phenotype matching, in which case individuals could possibly bias social behaviour towards their paternal close kin as well as their maternal kin.

Although these positive yet weak relationships between associations and biparental relatedness in female eastern grey kangaroos have been found, there are a number of questions remaining about kin structuring in this species. It is unclear to what extent these social patterns are explained by kangaroos associating with kin with which they are familiar (such as mother and maternal sisters), versus due to females discriminating unfamiliar (i.e. paternal) kin through phenotype matching. We also do not know how the relationship between kinship and association patterns in a population may change depending on whether all females or only females of breeding age are considered, since the associations of sub-adult females can influence these population-wide measures (Godde et al. 2015). Similarly, although we have previously demonstrated that pairs who associate more frequently than expected from their space use overlap (referred to as 'preferred associates') are significantly more closely related than expected (Best et al. 2014), it is unclear if this pattern remains significant among adult females alone. Based on this previous research, our current study had two broad objectives. First, we predicted that post-weaning relationships between mothers and their sub-adult daughters would have a strong influence on the positive correlations between pairwise association strengths and genetic relatedness. We tested this by exploring correlations between these measures over four consecutive years, using both biparental (microsatellite-based) and maternal (mitochondrial marker and observational pedigree) measures of relatedness, when

including sub-adults and when considering only adult females. We also considered pairwise spatial overlap in these analyses. Second, we predicted that kinship would be a significant driver of preferential associations between females. We investigated the extent to which females showed preferential relationships with biparentally-related female kin over two two-year time periods, both when sub-adults were included in the dataset and when they were omitted.

Methods

Field data collection

Fieldwork was conducted between January 2010 and December 2013 at a 37.4 hectare site within Sundown National Park (28°55'03''S, 151°34'46''E), Queensland, Australia. Each year around 200 female eastern grey kangaroos (hereafter, 'kangaroos'), and a smaller number of males, grazed regularly within the study area, with approximately 290 different females identified over four years. Individuals were recognized based on their natural markings and features, as done in other studies of this species (Jarman et al. 1989; Carter et al. 2009; Best et al. 2013). Association survey data were collected over 10 to 14 days each month, following the methods of Best et al. (2013, 2014). Surveys were conducted approximately two hours after sunrise and two hours before sunset, and involved the researcher walking through the study site in a haphazard manner and identifying the female kangaroos that were foraging within the site. For each kangaroo seen during a survey, the number of adult and sub-adult females in her temporary foraging group was counted. The 15 metre chain rule was used to assign group membership, by which any individual in a group had to be within 15 m of at least one other group member (Jarman 1987). The identities of all females within a group were recorded, and all group members were assumed to be associating, following the 'gambit-of-the-group', (Whitehead and Dufault 1999). GPS coordinates of each group (or, in groups with widely dispersed members, approximate GPS coordinates for individuals) seen during a survey were taken using a Garmin eTrex H GPS device (Garmin International Inc, Olathe, KS, U.S.A.). Between January 2010 and August 2012, additional GPS locations for females were taken on an opportunistic basis whenever individuals were encountered during non-survey field sessions.

Females' reproductive states were recorded at each observation, as described by Best et al. (2015) and in Chapter 2 of this thesis. For young that survived to permanent emergence from the pouch (PEP), we recorded the month of PEP and assumed young to be weaned eight months after PEP (Poole 1975), unless they were seen nursing at a later date (although this was rare). Females that had been weaned but had not yet reached breeding age were categorized as sub-adults. Females in

this population were first observed to breed at an average of 30.9 months (± 6.2 months, N = 42) after PEP. We considered all females capable of breeding after this average age, and they were recorded as adults at this age, unless they had already begun breeding (in which case they were recorded as adults when a small pouch-young was first observed).

Quantifying associations

For each calendar year, a matrix of pairwise association indices among females based on their half-weight indices (HWI) (Cairns and Schwager 1987) was generated from association survey data using the software SOCPROG2.4 (Whitehead 2009), as described by Best et al. (2013) and in Chapter 2. In each matrix, we included females recorded on surveys more than ten times in that year, excluding females seen less frequently in order to minimize potential bias in association indices caused by low numbers of observations (Whitehead 2008). Applying these restrictions resulted in the following yearly numbers of females being included in the matrices of association indices (with the mean ± standard deviation number of survey records per female in parentheses): 2010 N = 126, (46.8 ± 26.4 records/female); 2011 N = 160 (62.0 ± 37.5 records/female); 2012 N = 145 (41.0 ± 20.3 records/female; 2013 N = 150 (43.4 ± 22.2 records/female).

To quantify pairwise preferential associations, association survey data were pooled for two consecutive two-year periods (2010-2011 and 2012-2013). From these survey data, we calculated pairwise association indices for females observed on surveys more than ten times and for whom we had 50 or more GPS locations (N = 113 in 2010 – 2011 and N = 107 in 2012 – 2013). GPS points were only taken when animals were foraging in our study area, as were association records, so that while these GPS points do not describe complete home ranges, the two sets of data were collected in the same locations. For this analysis, we used the HWIG association index, which is based on the HWI but controls for differences in individuals' gregariousness (Godde et al. 2013). Following the method described by Best et al. (2014), we used the R package Digiroo2 (Dwyer et al. 2013) to create 200 simulated pairwise association indices based on individuals' space use alone. If a pair's observed HWIG was within the top 2.5% of the distribution of their simulated association indices, we considered that they associated more frequently than expected by chance, and termed them preferred associates. Pairs with observed association indices within the bottom 2.5% of expected HWIGs were said to avoid each other, and pairs with observed association indices within these extremes were classed as casual associates.

Genetic relatedness measures

To estimate pairwise biparental relatedness among females, fresh fecal samples were collected in the field from all the majority of individuals within the study site (including males, females, and young). DNA was extracted and amplified by PCR using the method described by Best et al. (2013), and individuals were genotyped at up to twelve polymorphic microsatellite loci. Two hundred and fifty-eight individuals were typed at eight or more of these loci, and pairwise genetic relatedness coefficients among these individuals were estimated using the method of Queller and Goodnight (1989). To help identify mother-daughter pairs within the population that were not known through behavioural observations, we used maternally inherited mitochondrial DNA (mtDNA) sequences to identify haplotype groups in genotyped females. A 566 base pair fragment of the mtDNA control region had been previously sequenced for 103 females (Best et al. 2013; Coghlan 2013), with three different haplotype sequences reported for these females. This gave a total of 160 females whose mtDNA haplotype was known and who had been genotyped at eight or more microsatellite loci. These genetic data were then used to identify mother-daughter pairs among females that were adults when preliminary field observations began in September 2009. First, we calculated the mean (and standard deviation) biparental relatedness estimate for 57 known mother-daughter pairs (mean = 0.440 ± 0.135). We then considered all other pairs of females with a biparental relatedness measure of greater than 0.30 (i.e. values greater than one standard deviation below the mean) to be 'potential mother-daughter pairs', except when known pedigrees from behavioural observations meant that they could not be mother and daughter. Only the pairs for which the mtDNA haplotypes of both members were known were included in parentage analysis. While it is possible that mother-daughter relationships existed amongst the females that were excluded, in our subsequent analyses we wanted to be as clear as possible in differentiating which pairs were mother and daughter and which were not. From the candidate potential mother-daughter pairs for which haplotypes of both members were known, we eliminated pairs where members did not share a mtDNA haplotype. This gave 100 pairs with biparental relatedness estimates greater than 0.30 in which both individuals had the same mitochondrial haplotype. We used the microsatellite data from these pairs to perform single-parent analysis using the program CERVUS 3.0 (Kalinowski et al. 2007), since few adult males (potential fathers) had been genotyped. The mean proportion of loci typed was 0.925 from the twelve microsatellite loci. A simulation of parentage analysis was performed based on the allele frequency data using 111 candidate mothers and 10,000 offspring. These data were then used for parentage analysis of the potential mother-daughter pairs. Twenty-eight pairs had positive LOD scores with strict confidence levels (95%) for their Delta scores, and we considered these pairs to be mother and daughter in subsequent analyses.

The remaining seventy-two candidate pairs that did not meet these criteria were considered to not be mother and daughter.

Foraging range overlap

We used GPS locations to estimate individuals' foraging ranges within the study site using the kernel density estimate (KDE) method. For females observed on surveys more than ten times and with at least 30 GPS fixes in a given year, we calculated the 95% volumes of intersection (VI) of their foraging ranges with those of all other females using the R package Digiroo2 (Dwyer et al. 2013). These pairwise measures of overlap were the mean of the measures for each female in a pair.

Data analyses

Biparental relatedness and pairwise associations

To assess the influence of biparental relatedness on association patterns, the HWI matrices for each year were edited to remove females that had not been genotyped at eight or more microsatellite loci. We created edited versions of the biparental genetic relatedness matrix for each of the four years that included only the females included in the association matrix for that year. Each year, the edited matrices included between 80% and 89% of the adult and sub-adult females recorded on association surveys more than ten times that year (2010, N = 101 females; 2011, N = 136; 2012, N = 126; 2013, N = 134). Thus for each year we had a pair of matrices with identical row and column labels (kangaroo IDs). Using the ade4 package (Dray and Dufour 2007) in the R statistical software program (R Core Team 2013), each matrix in a pair was converted to a distance matrix. These matrices were then subjected to a Mantel test (non-Euclid, Monte Carlo test) with 999 permutations, to determine the strength and significance of the correlation between the two matrices. To calculate correlations between HWIs and relatedness among adult females only, truncated versions of both matrices were created for each year with sub-adult females removed. For these matrices, we assigned sub-adult status to any female that had been weaned in that year or in the last six months of the previous year, unless they were observed with a pouch-young.

Maternal relationships and pairwise associations

To explore the relationship between mother-daughter status and pairwise association strength, we created pairs of matrices for each year that included all females recorded on association surveys more than ten times that year which were genotyped at eight or more microsatellite loci and had known mtDNA haplotypes (daughters known thorough behavioural observations were assumed to have the same mtDNA haplotypes as their mothers, and were also included). These matrices contained the majority of females genotyped at 8 or more microsatellite loci, and between 71% and

80% of all females observed more than 10 times on association surveys in a given year (2010, N = 98 females; 2011, N = 118; 2012, N = 113; 2013, = 120). One matrix contained pairwise association indices (HWIs) and the other was a binary matrix indicating whether each pair of females was mother and daughter (0 = no, 1 = yes), the latter based either on observational pedigrees or on the genetic analyses described above. We then performed Mantel tests with 999 permutations to examine the relationship between the two matrices for each year. Similarly to the previous analyses, we then removed sub-adults from each matrix in each year (sample sizes: 2010, N = 76; 2011, N = 98; 2012, N = 100; 2013, N = 114) and repeated the Mantel tests on these truncated matrices.

Biparental relatedness, associations, and spatial overlap

Pairwise home range overlap data were used to determine whether relationships between biparental kinship and pairwise association strength were significant when controlling for the influence of spatial overlap on associations. For each of the four years, three matrices were created, each containing the same individuals as row and column labels: one contained pairwise association indices, one contained pairwise biparental relatedness estimates, and one contained pairwise proportions of foraging range overlap. Individuals included in these matrices needed to have been recorded on association surveys >10 times in a year, genotyped at eight or more microsatellite loci, and have 30 or more GPS locations recorded in that year. These restrictions gave the following sample sizes: 2010, N = 68; 2011, N = 106; 2012, N = 83; 2013, N = 89. For each year, a partial Mantel test was conducted to assess the significance of the relationship between association and genetic relatedness while controlling for the influence of foraging range overlap on these two parameters. This analysis was repeated with sub-adult females removed from both matrices, using the following sample sizes: 2010, N = 59; 2011, N = 85; 2012, N = 58; 2013, N = 75.

Biparental relatedness and preferential associations

To determine if biparental relatedness was associated with preferential associations, and whether this correlation varied between the two two-year periods, we generated pairs of matrices for each of two non-overlapping two-year time periods (2010 - 2011 and 2012 - 2013). One matrix was a binary matrix of preferential/non-preferential association status among pairs of females (based on Digiroo2 analyses and with the non-preferential category including both casual associates and avoidances), and the other was a matrix of pairwise biparental relatedness estimates. For 2010 - 2011 we had biparental relatedness data for 108 of the 113 females included in the Digiroo2 analyses, and for 2012 - 2013 we had relatedness data for 100 of the 107 females. We performed Mantel tests between the binary matrix of preferred associations and the genetic relatedness matrix

from each time period, with 999 permutations for each analysis. As for the previous analyses, sub-adults were removed from the matrices and the Mantel tests were repeated using adults only (sample sizes: 2010 - 2011, N = 85; 2012 - 2013, N = 88). In this case, any female weaned during the two-year time period was considered to be a subadult. In addition, we counted the number of known mother-daughter pairs present in the population during each time period (both adult-subadult and adult-adult dyads), and calculated the proportions of these pairs that associated preferentially.

Results

Pairwise associations and kinship

When both adult and sub-adult females were included, pairwise HWIs and biparental relatedness estimates were weakly yet significantly positively correlated in each of the four years (Mantel tests using the Pearson correlation: 2010 r = 0.130; 2011 r = 0.125; 2012 r = 0.101; 2013 r = 0.081, all p-values = 0.001), with a trend towards progressively weaker correlations over time (Figure 1). Omitting sub-adults resulted in weaker relationships between association strengths and pairwise associations in each year, but the relationships remained significant (Mantel tests: 2010 r = 0.111; 2011 r = 0.092; 2012 r = 0.082; 2013 r = 0.066, all p-values = 0.001). Known mother-daughter pairs comprised approximately 0.4% of all female pairs in each of the four years. Females' pairwise binary mother-daughter status (no = 0, yes = 1) was positively correlated with pairwise HWI in each year when females of all ages were considered (Mantel tests: 2010 r = 0.316; 2011 r = 0.346; 2012 r = 0.292; 2013 r = 0.278, all p-values = 0.001) (Figure 2). These correlations weakened but remained positive and significant when sub-adults weaned that year were omitted from the matrices (Mantel tests: 2010 r = 0.215; 2011 r = 0.178; 2012 r = 0.192; 2013 r = 0.260, all p-values = 0.001).

Spatial overlap, associations, and kinship

When the influence of foraging range overlap on the correlations between the association and relatedness matrices was controlled for, pairwise association strength and genetic relatedness were still significantly but weakly correlated (partial Mantel tests: 2010 r = 0.093; 2011 r = 0.100; 2012 r = 0.093; 2013 r = 0.085, all p-values = 0.001). When we included only adult females in the analyses, there were only very weak positive correlations between association strength and genetic relatedness when we controlled for foraging range overlap, which were not consistently significant across the years (partial Mantel tests: 2010 r = 0.053, p = 0.034; 2011 r = 0.048, p = 0.014; 2012 r = 0.029, p = 0.133; 2013 r = 0.023, p = 0.153).

Preferential associations and kinship

In both two-year time periods, mothers and daughters preferentially associated more frequently than not. In 2010 - 2011, 29 out of 46 mother-daughter pairs were preferred associates of each other, while in 2012 - 2013, 27 out of 35 mother-daughter pairs were preferred associates. Despite this, biparental pairwise relatedness was only weakly (yet significantly) positively correlated with pairwise preferential association status in each time period (Mantel tests: 2010 – 2011 $r = 0.094$, $p = 0.001$; 2012 – 2013 $r = 0.082$, $p = 0.001$). When sub-adults were excluded from the analyses, these correlations weakened (Mantel tests: 2010 – 2011, $r = 0.048$, $p = 0.006$; 2012 – 2013, $r = 0.062$, $p = 0.003$).

Discussion

Close associations amongst philopatric same-sex relatives, either between or within generations, are one way that sociality can develop, and such relationships are common in many species of mammal (Gompper et al. 1998; Silk 2007). We examined the contributions of kinship to association patterns in a gregarious herbivore with female-biased philopatry but without cooperative behaviours. Biparental genetic relatedness explained only a small proportion of females' pairwise association strengths over four consecutive years, and this proportion was even lower when considering only adult pairs. When the influence of pairwise overlap of foraging ranges on the relationship between these variables was controlled for, biparental relatedness was even less strongly correlated with association strengths. Although matrilineal kinship did not explain a large proportion of association strengths, mother-daughter relationships were often strong even into adulthood, shown by the more than half of such pairs that associated preferentially (i.e. significantly more frequently than expected based on their space use overlap).

Post-weaning associations between mothers and their sub-adult daughters have been reported in several social and semi-social macropods, including eastern grey kangaroos (Stuart-Dick 1987; Jarman 1994), red-necked wallabies (*Macropus rufogriseus*) (Johnson 1989), and euros (*Macropus robustus*) (Ashworth 1995). However, these studies have not addressed whether the frequencies of such associations are explained by temporal and spatial overlap between mothers and their daughters, or represent an active choice to associate with kin. In addition, few macropod studies have explored how the strengths of mother-daughter relationships may change once daughters reach adulthood themselves. Here, we have shown that the binary mother-daughter status of pairs is significantly related to pairs' association indices, even when restricting our samples to females of

breeding age. However, considerable variation was apparent in association strengths among mother-daughter pairs in our study within individual years, both for sub-adults and adult daughters. Despite the fact that all females experienced similar ecological conditions such as resource availability and population density during a given year, not all female kangaroos with adult daughters associated with their daughters at the same rate. Several factors may explain this, and these could be investigated in more depth in future work.

Within our population, some females had several adult and/or sub-adult daughters, while others had none or only had one daughter. A mother's subsequent reproductive events may influence her relationships with her older daughter; for example, if a female weans a second daughter, she may associate more strongly with her newly weaned offspring than with her older one. This has been reported in bison, where mothers and their weaned daughters associated less closely after the mother's next young was born (Green et al. 1989). Our data collection period was not long enough for us to quantify how mother-daughter relationships changed from when the daughter was weaned to when she weaned her own offspring, but this is something that could be investigated with additional years of study. In addition, older mothers may associate differently with their daughters than younger mothers do, and this age difference might contribute towards some of the variation in mother-offspring association strengths in our population. In other ungulates with female philopatry, the ages of both the daughter and the mother have been found to influence the strengths of their relationships. In a high-density population of red deer, and in mountain goats (*Oreamnos americanus*), older mothers associated less strongly with their daughters than did younger mothers (Albon et al. 1992; Godde et al. 2015). Alternatively, females' propensities to associate with their daughters may be consistent across multiple offspring. Indeed, maternal style has been proposed to reflect a dimension of animal personality (Koski 2014). Additional research in this population could focus on exploring whether differences between mothers in their associations with daughters are consistent over multiple offspring.

If post-weaning mother-daughter relationships involve a benefit to the offspring, they may represent a form of extended maternal care. This has been suggested for bison, where young females that grouped with their mother had greater spatial centrality within the group and also experienced fewer displacements by other animals (Green et al. 1989). Female yearling bighorn sheep may also have benefitted from post-weaning associations with their mothers, by tending to grow more rapidly than yearlings that did not associate with their mothers (L'Heureux et al. 1995). In female eastern grey kangaroos, Jarman (1994) reported that young females with mothers in the population began breeding earlier, and had greater survival to weaning of their first two offspring, than females

without mothers, although the association strengths of these mother-daughter pairs were not considered. Continued association with a sub-adult daughter may also represent a form of maternal investment, if the mother incurs fitness costs. Female red-necked wallabies (*Macropus rufogriseus*) were less likely to be successful in their subsequent breeding attempt if they maintained strong associations with their offspring of either sex in the six months following weaning (Johnson 1986). This reduced reproductive output was thought to be a result of food competition facilitated by increased social tolerance of relatives. It would be interesting to investigate the costs and benefits of post-weaning associations to both mothers and their daughters in our study population, and to see if the balance of these costs and benefits varied with ecological conditions.

We observed a weak correlation between pairwise association strengths of adult and sub-adult females and biparental genetic relatedness; this pattern was relatively stable over the four years of study and mirrored the previous findings of Best et al. (2014), that were based on a two-year period of observations in the same population. In the current study we conducted additional analyses that included only adult females, and obtained similar results to when sub-adults were included, although with slightly weaker correlations in each instance. These lower correlation coefficients when sub-adults were removed from the analyses should be interpreted with caution, and may be caused by the decrease in the size of the relatedness matrix caused by a reduced sample size. It is also possible that young females have close pairwise associations with their relatives that then weaken with age, although additional data would be needed to distinguish between these two interpretations. Nevertheless, our analyses showed that some degree of association with kin existed among females of breeding age. These correlations were similar to the patterns of weak genetic structuring seen among adult female kangaroos in a population at Wilsons Promontory National Park in Victoria (King et al. 2015b). This latter population had a higher density of kangaroos than both the current study population and the population studied at Wallaby Creek, in which moderate kin structuring was described by Jarman (1994). In some ungulates the strength of post-weaning associations between mothers and daughters can vary with population density, with the direction of this change depending on ecological conditions. In high-density populations of red deer (*Cervus elaphus*), spatial associations between mothers and their daughters were weak, with only young mothers and their youngest daughters having close spatial proximity to one another (Albon et al. 1992). These weak associations were potentially related to an increased propensity for dispersal of sub-adult females at higher densities. The inverse relationship between density and mother-daughter associations was seen in bighorn sheep (*Ovis canadensis*), where yearling females were more likely than expected to be group mates or nearest neighbours with their mothers only in years when the population was at a high density (L'Heureux et al. 1995). It is possible that population density in

eastern grey kangaroos could modulate both the associations among mothers and their daughters and among adult female relatives, since there may be greater benefits to associating with kin at lower population densities.

If female kangaroos recognize and bias their social behaviour towards kin, this social preference could be reflected in measures not captured by pairwise association indices – for example, females may show less aggression towards kin, as seen in female Iberian red deer (*Cervus elaphus hispanicus*) (Ceacero et al. 2007) and in ground squirrels (*Spermophilus* spp.) (Holmes and Sherman 1982). Preferentially reducing the rate or intensity of aggressive behaviour towards relatives (over unrelated individuals) can be seen as a form of kin selection (Hamilton 1964), although little evidence for this exists for mammals (Smith 2014). Nevertheless, female tammar wallabies (*Macropus eugenii*) were less aggressive towards relatives than towards unrelated individuals, even though affiliative behaviours did not differ between kin and non-kin (Blumstein et al. 2002). Similar mechanisms of favouring kin may occur in eastern grey kangaroos, and although instances of female aggression tend to be infrequent in wild populations (Grant 1973), increased social tolerance of kin while foraging could be investigated in future work.

Due to the lack of information on paternity in our kangaroo population, we were unable to test for differences in association strengths among maternal, paternal, and non-relatives, as other studies on kin-biased social behaviour in mammals have done (e.g. Smith et al. 2003; Wahaj et al. 2004; Perry et al. 2008). Instead, we compared pairwise association strengths to both a continuous measure of biparental genetic relatedness and a binary measure of pairwise mother-offspring status, to attempt to look at the separate effects of biparental and maternal kinship. Although it is possible that female kangaroos might also associate strongly with their maternal half-sisters, recognizing them through familiarity via mutual associations with their mother (Tang Halpin 1991), neither our genetic nor behavioural data were sufficient to infer all these sib-ships. With additional years of data collection at our study site, future studies could extend the maternal kin category to include full- and half-sisters, and compare the strengths of these relationships to those among biparental kin.

It should be noted that although the full and partial Mantel tests used in this study are commonly employed in biology to assess correlations between pairwise association strengths and estimates of genetic relatedness (e.g. Frère et al. 2010; Chiyo et al. 2011; Carter et al. 2013; Best et al. 2014), this approach is not without its limitations. Guillot and Rousset (2013) showed using simulated data that when spatial autocorrelation is present in the data, the full Mantel test rejects the null hypothesis too frequently, and the partial Mantel test can also be influenced by this same bias. The

spatial autocorrelation of our data should be considered when interpreting the significance of the correlations that we have reported, and future studies could explore an alternative way of assessing the correlations between matrices of variables.

In summary, although a weak relationship existed between kinship and association strengths among our adult female kangaroos, we have shown that mothers and their adult daughters sometimes continued to associate closely, and often more frequently than expected based on their spatial overlap alone. However, there was considerable variation in these mother-daughter association strengths. Future studies should aim to separate out the influences of maternal versus paternal kinship on association patterns among kangaroos, and explore the variables that may affect mother-daughter association strengths following weaning.

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Figure legends

Figure 1. Scatterplots of the relationship between biparental genetic relatedness estimates and association strengths (half-weight indices) for adult and sub-adult female kangaroos, in four consecutive years (sample sizes: 2010 N = 101; 2011 N = 136; 2012 N = 126; 2013 N = 134).

Figure 2. Box-and-whisker plots of the relationship between known mother-daughter status of dyads (0 = not mother and daughter, 1 = mother and daughter) and association strength (half-weight index) for adult and sub-adult female kangaroos, in four consecutive years (sample sizes: 2010 N = 89; 2011 N = 118; 2012 N = 113; 2013 N = 120). The black line represents the median value, and the upper and the lower boxes either side of this represent the upper and lower quartiles respectively. The top and bottom whiskers represent the maximum and minimum values (respectively) when outliers are excluded. Outlying data points are represented as open circles.

Figures

Figure 1

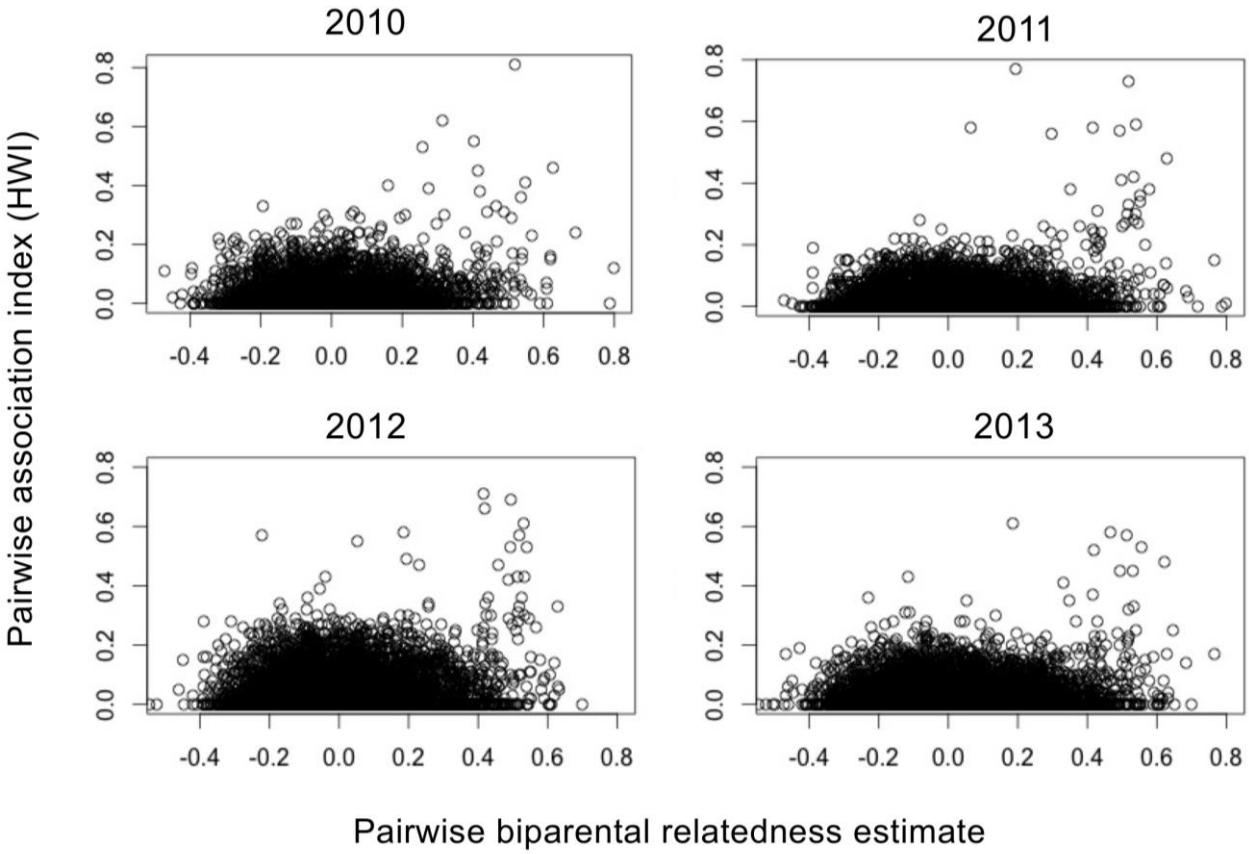
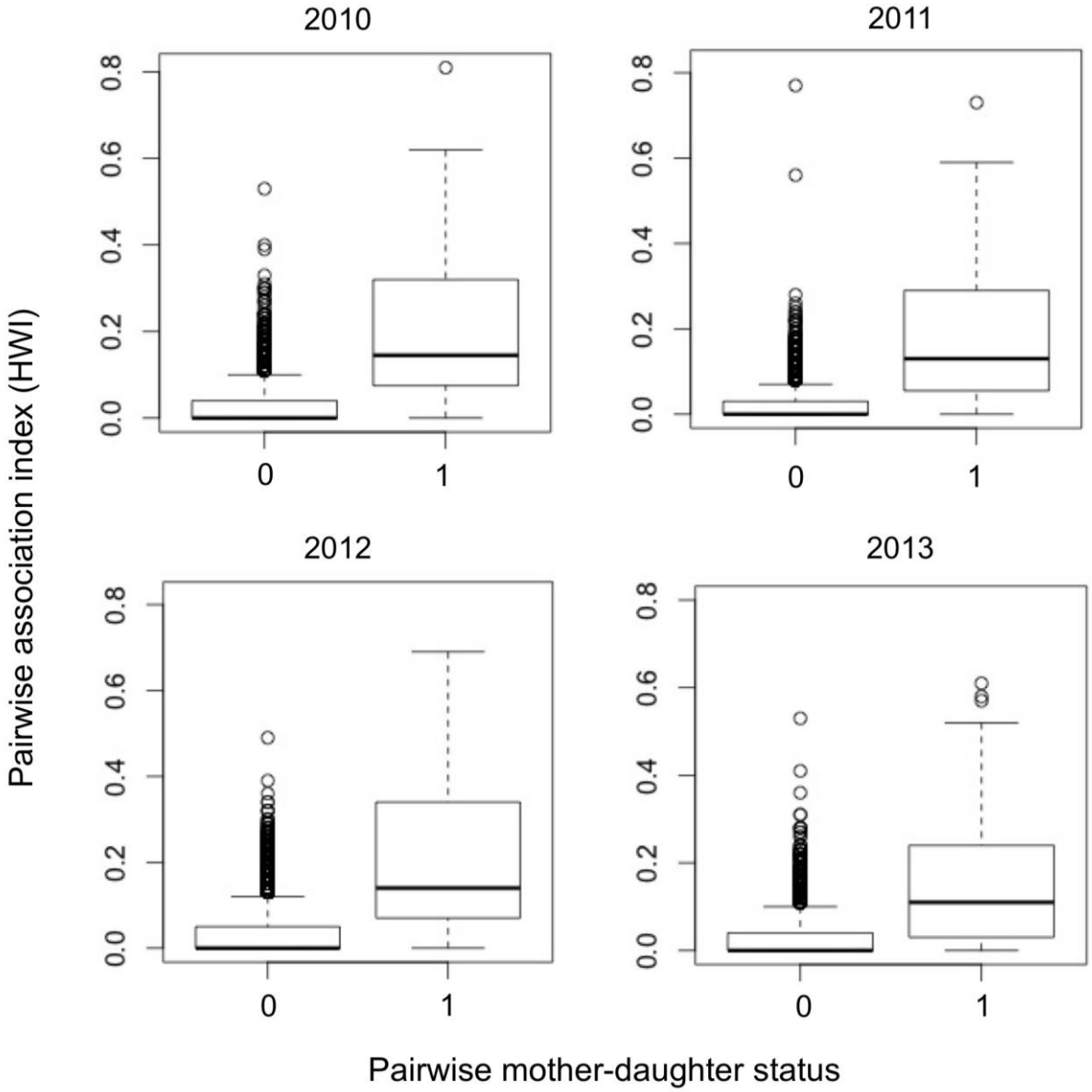


Figure 2


2010
2011
2012
2013
Pairwise association index (HWI)
Pairwise mother-daughter status
0.0
0.2
0.4
0.6
0.8
0
1

Intrinsic and environmental predictors of short-term fluctuations in female kangaroos' sociability traits

Menz, C. S., Goldizen, A. W., Freeman, N. J., Blomberg, S. P., and Best, E. C.

Abstract

Group-living vertebrate populations that show high temporal flexibility in the sizes and compositions of groups are described as having higher fission-fusion dynamics in their sociality. This form of social organisation allows individuals to freely join and leave groups, depending on whether the costs of grouping outweigh the benefits. Ecological conditions, as well as individuals' short- and longer-term intrinsic characteristics, can influence individuals' levels of sociability, broadly defined as the ways in which they interact with conspecifics. Although some studies on species with higher fission-fusion dynamics have shown that environmental conditions and/or individuals' states can relate to individuals' sociability, multiple different behaviours have been studied as measures of sociability, and there is little known about how constantly changing characteristics of individuals might affect these dimensions of sociability. In addition, the combined influences of multiple short-term environmental and intrinsic variables on sociability measures have rarely been explored. In this study, we investigated how shorter-term environmental conditions and states of individuals related to two broad aspects of females' individual sociability in a wild population of eastern grey kangaroos (*Macropus giganteus*). Each month over a five-year period, we analysed how these temporally unstable variables related both to individuals' grouping patterns (to reflect general gregariousness) and to the number of different conspecifics with which an individual associated (a measure of 'choosiness' of social partners) for over 100 adult females. Rainfall interacted with individuals' body condition to influence females' mean monthly group sizes and distance that females foraged from their nearest neighbours, while the numbers of different conspecifics that a female grouped with was lower when females had older dependent young. Although social preferences exist among females in this population, and females' measures of sociability are repeatable and differ among individuals over the long term, these current findings suggest that the synergistic influences of individual state and environmental conditions cause short-term changes in females patterns of sociability over shorter periods.

Introduction

Individuals within a species or population often differ consistently in their sociability, or how they respond to and interact with conspecifics. Sociability has been described as one of the five key

dimensions of animal personality (Réale et al. 2007), and individual differences in this trait can relate to outcomes linked to fitness, such as natal dispersal patterns (Cote and Clobert 2007; Blumstein et al. 2009), reproductive success (Silk et al. 2003; Cameron et al. 2009; Vander Wal et al. 2015), and survival and longevity (Silk et al. 2010; Stanton and Mann 2012; Weiss et al. 2013). There are many ways in which sociability has been measured in vertebrates, although there is uncertainty over whether different measures are components of a single personality trait, or multiple separate traits (Koski 2014). Aspects of individuals' sociability can be considered as relating to two general categories – general gregariousness, and relationships with particular other individuals. Gregarious tendency does not relate to the specific individuals associated with, and has been quantified in various ways, including preferred group size (Cote et al. 2012) and distance to nearest neighbours (Sibbald et al. 2005). In contrast, measures such as the quality and numbers of social relationships or 'bonds' that animals form does consider the specific identifies of other individuals (Silk 2007). Social network analysis has also been increasingly used within the last decade to provide information about the numbers and strengths of individuals' relationships (Wey et al. 2008; Sih et al. 2009; Makagon et al. 2012). Various metrics of individuals' direct and indirect connectedness within a population can be calculated from a social network, and these have been used as aspects of sociability (for example, Jacoby et al. 2010; Barocas et al. 2011; Wey and Blumstein 2012).

The adaptive value of sociability for individuals has been a growing topic of research during recent years. There is evidence in primates that females who are more socially integrated can experience greater infant survival (Silk et al. 2003), greater adult longevity (Silk et al. 2010), and earlier onset of breeding (Charpentier et al. 2012). Similar benefits to reproductive success in highly sociable individuals have also been described some non-primate species, including those in which groups are not kin-based (Cameron et al. 2009), and in populations with non-stable group membership (Vander Wal et al. 2015). Although sociability is increasingly considered to confer fitness benefits in group-living species, some studies have reported fitness costs for individuals with high measures of sociability (Johnson 1986; Wey and Blumstein 2012), and have suggested that resource competition and density may be related to these costs. Therefore, it is likely that ecological conditions may influence whether sociability is costly or beneficial for individuals, and that measures of individuals' sociability within a group reflect this cost-benefit ratio. Changes in environmental conditions can influence various dimensions of sociability among members of a group. In a population of wild chacma baboons (*Papio hamadryas ursinus*), females formed strong relationships when food was scarce, but not when food was abundant (Henzi et al. 2009), suggesting that most social bonds between females may only exist when beneficial. Predation risk is

another ecological variable that can influence group sizes (Banks 2001) and temporal patterns of social organisation (Kelley et al. 2011). Population demographic factors can also affect the patterning of social relationships among group members. An increase in group or population size can lead to an overall reduction in the strengths and numbers of social relationships among its members, as demonstrated in yellow-bellied marmots (*Marmota flaviventris*) (Maldonado-Chaparro et al. 2015). Changes in group density can also influence the strengths of social connections among group members, as seen in red deer (*Cervus elaphus*) (Albon et al. 1992), although different classes may respond differently to these changes, as has been reported for sex classes in elk (*Cervus canadensis*) (Vander Wal et al. 2012). The composition of a group can also influence its members' sociability, as seen in chimpanzees (*Pan troglodytes*), where both resource aggregation and the number of females in estrus in the group were related to females' gregariousness (Wittiger and Boesch 2013). Sociability can also vary at the group-wide level with females' breeding cycles. For example, patterns of grooming and spatial proximity differed between the mating and birth seasons in free-ranging female rhesus macaques (*Macaca mulatta*) (Brent et al. 2013).

One strategy for reducing the costs and maximizing the benefits of sociability is for groups to change in size and composition depending on ecological conditions, a type of social organization known as 'higher fission-fusion dynamics' (Aureli et al. 2008) found in some primates and some other mammalian taxa. For example, temporary fissioning of a chimpanzee (*Pan troglodytes*) community into smaller foraging parties was thought to help individuals minimize the costs of time spent moving while retaining the benefits that a large, tightly bonded community can provide (Lehmann et al. 2007). Similarly, in spider monkeys (*Ateles geoffroyi*) and in chimpanzees, the distribution of food resources, which affected the travel time between patches, was related to feeding group sizes (Chapman et al. 1995). A social organization with higher fission-fusion dynamics allows individuals to make frequent decisions about how sociable to be and who to group with. It is likely that in addition to ecological variables affecting group-wide measures of sociability, individual animals' traits may also influence various aspects of their sociability.

Several stable attributes or traits of individuals, such as their sex, age class, and personality type, can relate to aspects of their sociability. For example, older female mouflon sheep (*Ovis gmelini*) associated less frequently with others than did younger females (Guilhem et al. 2000), with a similar trend in the roosting patterns of female northern long-eared bats (*Myotis septentrionalis*) (Patriquin et al. 2010). Measures of sociability have also been shown to correlate with various other dimensions of animal personality, including boldness (Pike et al. 2008; Croft et al. 2009; Michelana et al. 2009; Best et al. 2015) and aggressiveness (Godfrey et al. 2012; Lacasse and Aubin-Horth

2013). Consistent correlations between personality traits over time or across contexts are termed behavioural syndromes (Sih et al. 2004), and these correlations suggest that individuals may be constrained in their ability to show optimal levels of a trait such as sociability. Alternatively, the optimal levels of a trait may be different among individuals with different measures for other personality traits.

Shorter-term individual traits, such as reproductive state and condition, can also influence individuals' sociability. For example, female northern long-eared bats (*Myotis septentrionalis*) varied in the strengths of their associations with other females throughout their reproductive cycles, associating more closely during gestation than lactation (Patriquin et al. 2010). Reproductive state was also related to females' numbers of different associates within a Grevy's zebra (*Equus grevyi*) social network (Sundaresan et al. 2007), and to the strengths of associations among free-ranging beef cows (*Bos taurus*) (Finger et al. 2014). Both long- and shorter-term individual-based measures can interact to further regulate individuals' patterns of sociability. For example, body condition modulated the relationship between personality and grouping tendencies in female eiders (*Somateria mollissima*), a facultatively social bird (Öst et al. 2015). However, these studies have all focused on species in which reproduction is highly synchronous or seasonal, and we know little about how reproductive state influences measures of sociability in species in which females do not reproduce synchronously.

Species that exhibit higher fission-fusion dynamics are ideal for studying the ecological and intrinsic factors that can influence patterns of both aggregations and of social bonds in individuals. In species in which individuals can choose to join and leave groups as they want, the ability to be selective about social partners is likely to represent an aspect of sociability that is distinct from preferred group size. One such species is the eastern grey kangaroo (*Macropus giganteus*), a large-bodied marsupial that grazes in groups that frequently change in size and composition (Jarman 1994). Females do not reproduce synchronously, although some studies have reported seasonal peaks (Stuart-Dick 1987). Recent studies have shown that measures of individual females' sociability are stable over yearly or longer time-scales (Best et al. 2015; Chapter 2 in this thesis), although other evidence suggests that temporally unstable variables, both intrinsic and environmental, may influence individuals' patterns of sociability. In a population at Wallaby Creek in New South Wales, females with young that were approaching the age of permanent exclusion from the pouch were observed to be alone more frequently than expected (Jarman 1994). In addition, reproductive state influenced females' likelihoods of feeding in groups with adult males (Jarman 1994), so it is likely that grouping tendencies are influenced by reproductive state. Eastern

grey kangaroos feed almost exclusively on grass (Jarman and Phillips 1989), do not appear to engage in competition over this food resource, and females are rarely aggressive towards other adult females (Russell 1984), making them an ideal species in which to study sociability in the absence of agonistic and competitive interactions.

To investigate constraints on females' sociability, we tested whether a set of temporally unstable environmental and intrinsic variables, and their synergistic effects, were related to differences in measures of females' aggregation and association patterns. Our work had four broad aims. We investigated variables that influenced (1) females' mean foraging group sizes and (2) the average distances between females and their nearest neighbours while foraging. These approaches related to individuals' tendencies to aggregate, or their gregariousness. Based on previous observations in this species, we expected that females with larger young would be observed foraging in smaller groups and/or further from their nearest neighbours. We also predicted that food availability would be strongly related to rainfall, and that in conditions of higher food availability groups would be larger and females would forage further from their nearest neighbours. In addition, we tested whether a range of variables influenced 3) the number of different animals that females grouped with over a month and (4) the number of different nearest neighbours that females had. These final two aims relate to females' propensities to be selective or 'choosy' in their grouping patterns. We predicted that females would be less selective about their patterns of grouping and association during times of low food abundance, or when females are in poor condition or experiencing high energetic demand from lactation, and that females would consequently have higher numbers of group-mates and nearest neighbours during these times. Our rationale for these predictions is that when females are struggling to meet their energetic requirements, they would not be able to pay the extra costs incurred by increasing their movements to find and remain with their preferred companions.

Methods

Study site and population

Field observations were conducted from January 2010 until December 2014 at Sundown National Park, Queensland, Australia (28º55'03" S, 151º34'46" E), over 10 - 14 consecutive days each month. The study site was situated in a mixed habitat of grassy paddocks and open eucalypt woodland. Around 200 individual female eastern grey kangaroos (hereafter, "kangaroos") each year regularly foraged within the study site, with approximately 290 females identified over the five-year study period. A smaller number of adult and sub-adult males also used the study area, but were not

included in this study. Individual kangaroos were identified based on their natural features and markings (Jarman et al. 1989; Carter et al. 2009; Best et al. 2013). The region experiences cycles of droughts, but each year during the period of study, with the exception of 2014, the area received more rain than the average for the previous five years (2005 – 2009). Rainfall patterns varied widely from month to month, from a low of 2.8 mm in September 2012 to a high of 155.2 mm in February 2013. Rainfall data were taken from the Australian Bureau of Meteorology website for the Texas Post Office station (station number: 041100; 28°51'00" S, 151°10'12" E), approximately 40 km west of the study site. Food resources (grass) were quite evenly distributed throughout the paddock areas of the study area, although the availability of food varied considerably with rainfall. Rainfall lagged by one month was used as a proxy for availability of grass. Monthly estimates of green grass abundance were averaged across 110 quadrats (0.5 x 0.5 m) located 25 m apart along eight parallel transects that spanned the field site at 50 m distance from each other, and this estimate was highly correlated with rainfall lagged by one month (Pearson's product-moment correlation: $r = 0.73$, $p < 0.0001$).

Field data collection

Our social association surveys have been described previously (Best et al. 2013; Best et al. 2014). Briefly, during a morning or evening survey lasting approximately two hours, researchers walked through the study area recording the identities and group memberships of all adult and sub-adult females. The 15-metre chain rule was used to assign group membership, where each member had to be within 15 m of another group member to be considered part of the group (Favreau et al. 2010). The number of females in each group was counted, and all females were identified where possible. Young that were still nursing were not considered in counts of group sizes, as their grouping patterns were assumed to be very close to those of their mothers. From January 2012, we also recorded the identity of each female's nearest female neighbour in the group (that was not her dependent young), and estimated the distance in metres between these females. From October 2012 until December 2013, association surveys were conducted twice a day (once in the morning and once in the evening) for approximately one third of the surveys in each month. Two surveys on the same day were considered to be independent samples, since kangaroos move to shade to rest during the middle of the day, changing group memberships, before resuming feeding in the afternoon (Carter et al. 2009). In fact, foraging group memberships could change regularly within a survey session.

Each month, the reproductive states of all females seen within the study area were recorded, based on the observed presence and size of their pouch-young or young-at-foot. Reproductive state categories were the same as used by Best et al. (2015): NPY, a female with no visible pouch-young; SPY, a female with a small pouch-young; MPY, a female with a medium sized pouch-young; LPY, female with a large pouch-young that could exit the pouch but was not permanently excluded; YAF, a female with a young-at-foot that was permanently excluded from the pouch but still nursed; and SPY/YAF, a female with both a SPY and a YAF. Based on data on ages at first breeding for 34 females with known dates of PEP, young females that were known or estimated to have been weaned within the previous 20 months were categorized as sub-adults, unless observed to have begun breeding already. Each month, females' body condition indices were estimated visually from photographs as described by Best et al. (2015). Categories were 1 = poor, 2 = average and 3 = good, with category 3 combining Best et al.'s categories 3 and 4.

Data compilation

For each month from January 2010 until December 2014, we examined association survey records for females that had been recorded on eight or more surveys. For females recorded on more than eight surveys in a month, we randomly sub-sampled eight of those surveys, in order to ensure that we used the same number of data points for each female per month. In some months no females were observed on surveys eight or more times, and in months that did meet these sample size criteria for inclusion in the data set between 1 and 87 females were observed on eight or more surveys (average = 31.4 ± 22.0 females per month). Only adult females were considered in this data set, so we excluded sub-adults in a given month if they had not reached breeding age in that month. For each female-month included in the data set, we calculated the proportion of the 8 surveys that were conducted in the mornings compared to the afternoons, the mean foraging group size in which she was observed, and the mean distance between her and her nearest female neighbour (adult or sub-adult). We also counted the total number of different group-mates each female had in the 8 surveys each month, and the total number of different nearest neighbours that she had. For each month, we included the rainfall from the previous month and the body condition index and reproductive state (where these data were available) for each female.

Data Analyses

To address aims 1, 2, and 3, linear mixed effects models were run in the program R (R Core Team 2013) using the package lmerTest (Kuznetsova et al. 2014). Models were fit using restricted maximum likelihood (REML) with the Satterthwaith approximation for degrees of freedom. Subsequent ANOVA tests were conducted, and these test statistics are reported in the Results

section. We tested for colinearity among the explanatory variables by examining variance inflation factors (VIFs) in linear versions of the models that did not include the interaction terms or the random effects. None of the model variables VIFs greater than 4. This was deemed an acceptably low level of colinearity so all variables were retained in the models.

To address aim 1, we used data collected between January 2010 and December 2014 to look at factors affecting females' mean group sizes, with a sample size of 1202 monthly samples from 125 different females. Explanatory variables included the proportion of each female's eight samples in a month that were taken from morning survey records, the female's reproductive state and body condition, and the month and lagged rainfall (i.e. the previous month's total rainfall). We included interactions in the model between reproductive state and rainfall, and between BCI and rainfall. Female ID was included as a random effect.

For aim 2, we modeled the variables influencing females' mean nearest neighbour distances, using data from January 2012 until December 2014, with 485 monthly samples from 101 different females. We included the same variables as in aim 1, with the addition of a female's mean group size as an explanatory variable.

For aim 3, we used data from January 2010 until December 2014 and counted the number of different female group members an individual had across her eight sampled surveys in each month, with 2102 monthly samples from 125 females. The same set of variables was used in this model as in aim 1.

Finally, for aim 4 we counted the total number of different nearest neighbours each month that females had across their eight surveys, using 485 monthly samples from 101 different females from January 2012 until December 2014. This measure ranged from 1 to 8 and was considered as an ordered factor with eight levels. We ran the model using a cumulative link mixed model fit using the Laplace approximation (using the Hessian to compute standard errors of the model coefficients) with the 'ordinal' package in R (Christensen 2015). This model used the same set of variables as was used for aim 1, with the inclusion of females' mean group sizes and mean nearest neighbour distances as explanatory variables. We performed likelihood ratio tests using the ANOVA method to obtain significance values for the model parameters.

Results

Factors affecting females' mean group sizes (aim 1)

Over a five-year period of data collection, the mean monthly foraging group sizes in which females were observed during surveys ranged from 1.4 to 23.5. Females' mean group sizes were significantly influenced by month ($F_{11, 30} = 10.978$, $p < 0.0001$), although there was not a clear pattern across months. Reproductive state was a significant factor ($F_{5, 30} = 3.424$, $p = 0.004$), with the smallest mean group sizes for females with a LPY (Figure 1). The interaction between rainfall and females' body condition was significant (BCI * Rainfall: $F_{2, 30} = 18.132$, $p < 0.0001$). Females in poor condition (and, to a lesser extent, females in average condition) were found in smaller groups as rainfall increased, while females in good condition had larger average group sizes with higher rainfall (Figure 2). Neither the proportion of morning surveys included in females' monthly samples nor the interaction between reproductive state and rainfall were significant predictors of mean group size. The variance in the response variable attributable to the random effect (individual ID) for this model and the other three models are given in Supplementary Material.

Factors affecting females' nearest neighbour distances (aim 2)

On average, females were observed foraging at a distance of 6.19 ± 1.93 m from their nearest neighbour, and the mean nearest neighbour distances per female per month ranged from 0.71 m to 13.75 m. Females with larger mean group sizes foraged at significantly greater distances from their nearest neighbours than females with smaller mean group sizes ($F_{1, 31} = 6.242$, $p = 0.013$), and females had significantly different mean nearest neighbour distances in different months ($F_{11, 31} = 10.014$, $p < 0.0001$), although no seasonal trend was evident. There was no significant effect of the proportion of morning surveys in females' monthly samples. Nearest neighbour distance increased with higher rainfall ($F_{1, 31} = 20.135$, $p < 0.0001$) (Figure 3). Reproductive state trended towards significance, with females who had larger dependent young observed at a greater distance from their nearest neighbours ($F_{5, 31} = 1.937$, $p = 0.087$), with no significant interaction between rainfall and reproductive state. The interaction between body condition and rainfall was significant, where the positive linear relationship between mean nearest neighbour distance and rainfall was strongest for females in poor condition (BCI * Rainfall: $F_{2, 31} = 3.526$, $p = 0.030$) (Figure 4).

Factors affecting females' numbers of different group members (aim 3)

Individuals were observed in groups with an average total of 24.18 ± 11.08 different adult and sub-adult females across the entire period of data collection, with the number of different subadult and adult female group members per female per month ranging from 1 to 67. Mean group size was a very strong predictor of the number of different group members a female had in a month, with

females in larger groups also grouping with a larger number of individuals ($F_{1, 31} = 2360.20$, $p < 0.0001$). Month was significant ($F_{11, 31} = 13.65$, $p < 0.0001$), with females tending to have a greater number of different group members between June and December. Reproductive state was a significant variable in the model ($F_{5, 31} = 2.34$, $p = 0.039$), where females with a YAF (or a SPY and YAF) grouped with fewer different animals (Figure 3a). The interaction between reproductive state and rainfall was not significant. Females in average condition grouped with a greater number of different animals than those in poor or good condition, and body condition was a significant factor in the ANOVA ($F_{2, 31} = 5.000$, $p = 0.007$) (Figure 3b). Females grouped with fewer other animals in months with high lagged rainfall ($F_{1, 31} = 50.71$, $p < 0.0001$) (Figure 3c), but the interaction between body condition and rainfall was not significant.

Factors affecting females' numbers of different nearest neighbours (aim 4)

Females' numbers of different nearest neighbours each month ranged from 1 to 8. Individuals with larger mean group sizes had more different nearest neighbours (LR $stat_{1, 32} = 12.322$, $p < 0.0001$), as did females who foraged at greater distances from their nearest neighbours (LR $stat_{1, 32} = 4.026$, $p = 0.045$). The proportion of morning surveys included in females' monthly samples also influenced the different number of nearest neighbours an individual had, with females with a higher proportion of morning surveys in their samples having fewer different nearest neighbours (LR $stat_{1, 32} = 3.860$, $p = 0.049$). Females' numbers of different nearest neighbours were not significantly related to month, reproductive state, body condition or rainfall, or to the two interaction terms.

Discussion

The patterns of social relationships among group-living animals can vary with ecological conditions (e.g. Chapman et al. 1995; Henzi et al. 2009) and with population demographics (e.g. Maldonado-Chaparro et al. 2015). Individuals' conditions or states can also affect the ways in which they associate or interact with conspecifics (Sundaresan et al. 2007; Patriquin et al. 2010). Thus it is likely that external and intrinsic factors interact to fine-tune the balance of benefits and costs of being sociable somewhat differently for each individual in a population. In this study, we investigated variables that related to multiple facets of female eastern grey kangaroos' sociability. focusing on several short-term measures of individuals' aggregation and association patterns. Females' reproductive states and body conditions, and the interaction between body condition and rainfall, were significantly related to these measures of sociability, and the directions of these effects are described below.

The distribution and abundance of resources is a key ecological factor influencing group size in higher fission-fusion populations (Chapman et al. 1995; Lehmann et al. 2007; Smith et al. 2008). Other population-wide measures of sociability, such as strengths and stability of individuals' relationships, can also vary with resource availability (Henzi et al. 2009). We found that rainfall lagged by a month, which was a reliable proxy for grass availability, interacted with female body condition to affect females' mean monthly group sizes and nearest neighbour distances. As rainfall increased, females in poor condition (and, to a lesser degree, females in average condition) were observed in smaller foraging groups, while females in good condition were found in larger groups. All females foraged at greater distances from their nearest neighbours as rainfall increased, but the slope of this relationship was steeper for females in poor condition, with females in poor condition foraging the furthest from their nearest neighbours at times of high rainfall. This finding seems counterintuitive, given that food competition would presumably be lower in times of high rainfall, so females might be expected to be more tolerant of neighbouring group members being in close proximity. However, herbivores that are nutritionally stressed can prioritize feeding over other types of behaviour (e.g. Duncan 1985). Food stress may help explain the pattern observed in our population in which individuals in poorer condition may actively distance themselves from others to allow maximum foraging efficiency.

Rainfall also influenced females' selectivity about grouping partners, although this was not contingent on body condition. When we controlled for differences in monthly mean group sizes among individuals, we found that females grouped with significantly fewer different animals in months with higher lagged rainfall than in months with lower rainfall. This finding suggests that females can afford to be more selective about their associates during times of food abundance, but when food is scarce females do not maintain differentiated relationships as strongly, possibly because they need to spend more time looking for food. Our study did not consider the distribution of grass throughout the site, so it is unclear whether the distribution of food was uneven in times of low rainfall. Nonetheless, having to travel more frequently to find food patches could explain why females' choosiness of grouping partners could be limited in times of lower rainfall. Henzi et al. (2009) found that female chacma baboons' social relationships were less differentiated in times of higher food availability, the opposite pattern to our results. However, compared to the open-membership foraging groups of eastern grey kangaroos, baboon troops are more temporally and spatially cohesive (Melnick and Pearl 1986). It is possible that food abundance influences choosiness of social partners in different ways depending on the degree of fission-fusion dynamics and/or diet of a species. However, in giraffe (*Giraffa camelopardis*), herbivores with similar fission-fusion grouping dynamics similar to those of the eastern grey kangaroo (Carter et al. 2013),

females had a greater number of female associates (and stronger relationships with these associates) during the wet season than during the dry season. This suggests that constraints of food availability on sociability are likely to be more complex than we think, and further examination of these patterns across different species is needed.

We found that reproductive state influenced both females' aggregation and their association patterns. Females were found in significantly smaller groups on average in the months when they had large pouch-young than when they had small or no pouch-young. These results are similar to those of previous studies that have described female kangaroos tending to forage alone or in smaller groups around the time of pouch emergence of their young (Russell 1989; Stuart-Dick and Higginbotton 1989; Jarman 1994). This is thought to be a strategy to minimize the risk of a young becoming confused and following a female that is not its mother (Stuart-Dick 1987), as mother-offspring recognition appears to be poorly developed in this species (King et al. 2015). We also observed a trend for females to forage at greater distances from their nearest neighbours as their young grew older, although this was not significant. When controlling for the influence of females' mean group sizes on their numbers of different group members, we found that females with young-at-foot grouped with significantly fewer different individuals than did females with smaller dependent young or no young. This result suggests that, in addition to influencing females' aggregation tendencies, reproductive state may also affect their patterns of social relationships. The energetic costs of lactation are highest for female eastern grey kangaroos when their young are at the LPY and early YAF stages. Females with high lactation demands spent more time feeding and had higher bite rates than non-reproductive females at Serendip Sanctuary, Victoria (Cripps et al. 2011). At a different site in Victoria, Gélin et al. (2013) found that females with a LPY or YAF were significantly more likely to be observed feeding than were females with smaller or without pouch-young. Given this increased requirement to feed, we might expect that females with larger young may be less inclined to expend energy changing groups, and as a consequence be less choosy about their group mates, but we observed the opposite of this. Focal observations of females in different reproductive states to determine their patterns of joining and leaving might help explain this unexpected finding. We found no effect of reproductive state on females' numbers of different nearest neighbours, suggesting that the apparent increased choosiness of group mates of females with young-at-foot does not extend to being selective about who they forage next to.

The number of different nearest neighbours that females had in a month increased with their monthly mean group sizes, a relationship that we would expect to see if females were not demonstrating preferences for particular nearest neighbours. This further supports the idea that

females may be selective in relation to their social partners at the group-mate level, but not at the nearest neighbour level. This possibility should be further explored in future research. Although we did not expect aggregations or associations to vary significantly between morning and evening, we found that the number of morning surveys included in females' monthly sample data was a significant predictor of the number of different nearest neighbours. Kangaroos with more morning surveys had fewer different nearest neighbours than did kangaroos with fewer morning surveys. Several possible explanations exist for this observation. Kangaroos are known to continue grazing throughout the night (Clarke et al. 1995), and this may be the case in our population, or kangaroos may have begun foraging in the mornings before there was enough light to be able to commence our surveys. This could suggest that females' hunger levels were lower during the morning surveys than during the evening surveys (during which they had been resting in the shade for the majority of the daylight hours), and that they could be choosier about their nearest neighbours without being as constrained by nutritional requirements. If females had been grazing for at least some time before the morning surveys commenced, then it is also possible that they had already changed groups several times prior to the survey in order to locate a specific associate that they want to forage next to. Alternatively, differences in predation risk at different times of day could help explain why females had fewer different nearest neighbours in the mornings. Although dingos (*Canis lupus dingo*) were not present at the study site, red foxes (*Vulpes vulpes*) are known to prey on juvenile kangaroos (Poole 1982) and were occasionally seen during the daytime. Fox presence influenced kangaroos' foraging group sizes (although this depended in part on females' reproductive states) in a different study population (Banks 2001), so it is possible that predation risk could also shape other measures of kangaroos' sociability, such as their choosiness of nearest neighbours. At Elanda Point in Queensland, female kangaroos that foraged next to a female with whom they associated frequently were able to spend more time grazing and less time being vigilant than when foraging next to a less familiar associate (Carter et al. 2009). Hence, in our study population, it is possible that during the early mornings (when there is potentially the highest predation risk), females may benefit in a similar way by having few different nearest neighbours with which they have strong associations, rather than having a large number of different conspecifics as their nearest neighbours.

One variable that may be interesting to address in future studies is the age classes of females' nearest neighbours each month, and how this may affect measures of sociability. We included a female's neighbour whether she was an adult or a sub-adult, and this may have biased the results for females who had a sub-adult daughter with whom they still frequently associated. Future analyses could limit this sample to include only include the adult female neighbours of a focal individual. Similarly, another grouping variable that could be considered in the future is numbers and identities

of adult and sub-adult males within a group. Population density may also influence both the aggregation and association patterns of female kangaroos, and this would be interesting to investigate. Foraging group sizes of eastern grey kangaroos have been previously reported to increase exponentially as population density increases in an open forest habitat (Southwell 1984). We did not consider monthly estimates of population density in our analyses, since this was not determined in our study population, but it is possible that density may influence both the aggregation and association patterns of females. While non-random and preferential associations among some female kangaroos have been described in this population (Best et al. 2013; Best et al. 2014), average female association strengths were weaker in a high-density population (King 2015). How population density might interact with other variables that influence individuals' social patterns could be explored in future research.

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Figure Legends:

Figure 1. Predicted mean group size values (with 95% confidence intervals) for each level of female reproductive state. Reproductive state was a significant explanatory variable in the linear mixed-effects model. All other model fixed effects that are not graphed are set to their mean values.

Figure 2. Estimated parameter values from the linear mixed-effects model showing the interaction between the effects of BCI and rainfall on females' mean group sizes. This interaction was a significant explanatory variable in an ANOVA test. All other model parameters are set at their mean values in this figure. The three levels of BCI shown are: 1 = poor (solid line), 2 = average (dashed line), 3 = good (dotted line).

Figure 3. Estimated parameter values of significant fixed effects in the linear mixed-effects model. Predicted values (with 95% confidence intervals) for mean nearest neighbour distance as monthly rainfall increased. All other model parameters are set at their mean values in this figure. The effect of rainfall on females' mean nearest neighbour distances was significant in an ANOVA test.

Figure 4. Estimated parameter values from the linear mixed-effects model showing the interaction between the effects of BCI and rainfall on females' predicted mean nearest neighbour distances. This interaction was a significant explanatory variable in an ANOVA test. All other model parameters are set at their mean values in this figure. The three levels of BCI shown are: 1 = poor (solid line), 2 = average (dashed line), 3 = good (dotted line).

Figure 5. Estimated parameter values for variables predicting females' number of different group members in a month. All other model parameters are set to their mean values in each plot in this figure. (a) Predicted numbers of different group members (with 95% confidence intervals) for females in each of six levels of reproductive state. (b) Predicted numbers of different group members (with 95% confidence intervals) for females in each of three levels of BCI (1 = poor, 2 = average, 3 = good). (c) Predicted numbers of different group members (with 95% confidence intervals) with increasing monthly rainfall.

Figures

Figure 1

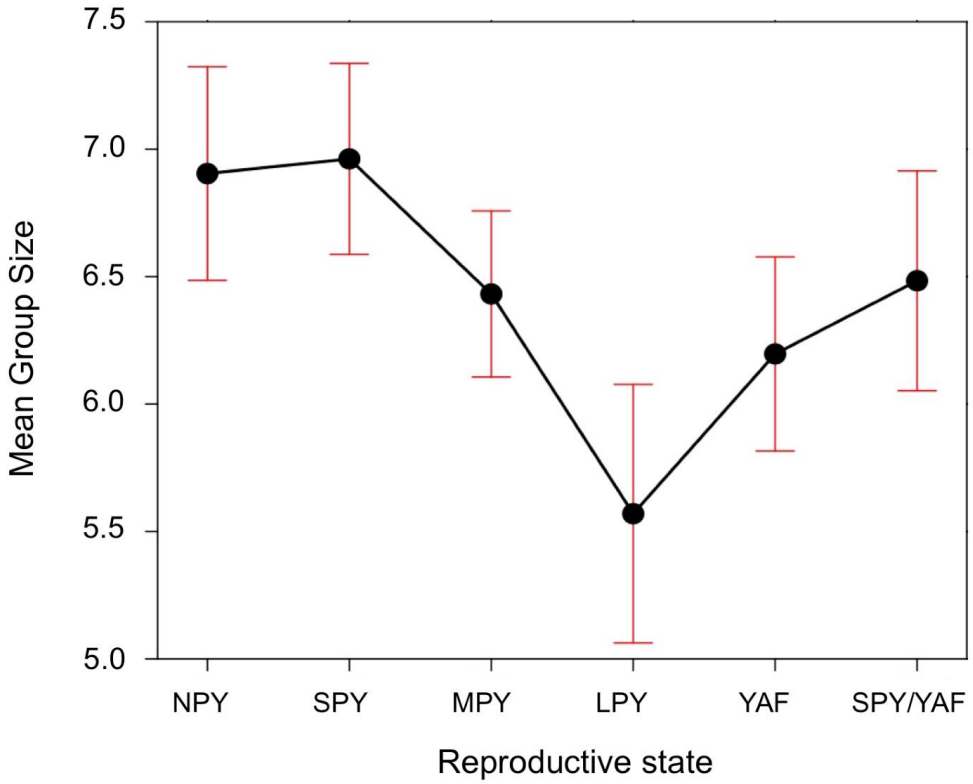


Figure 2

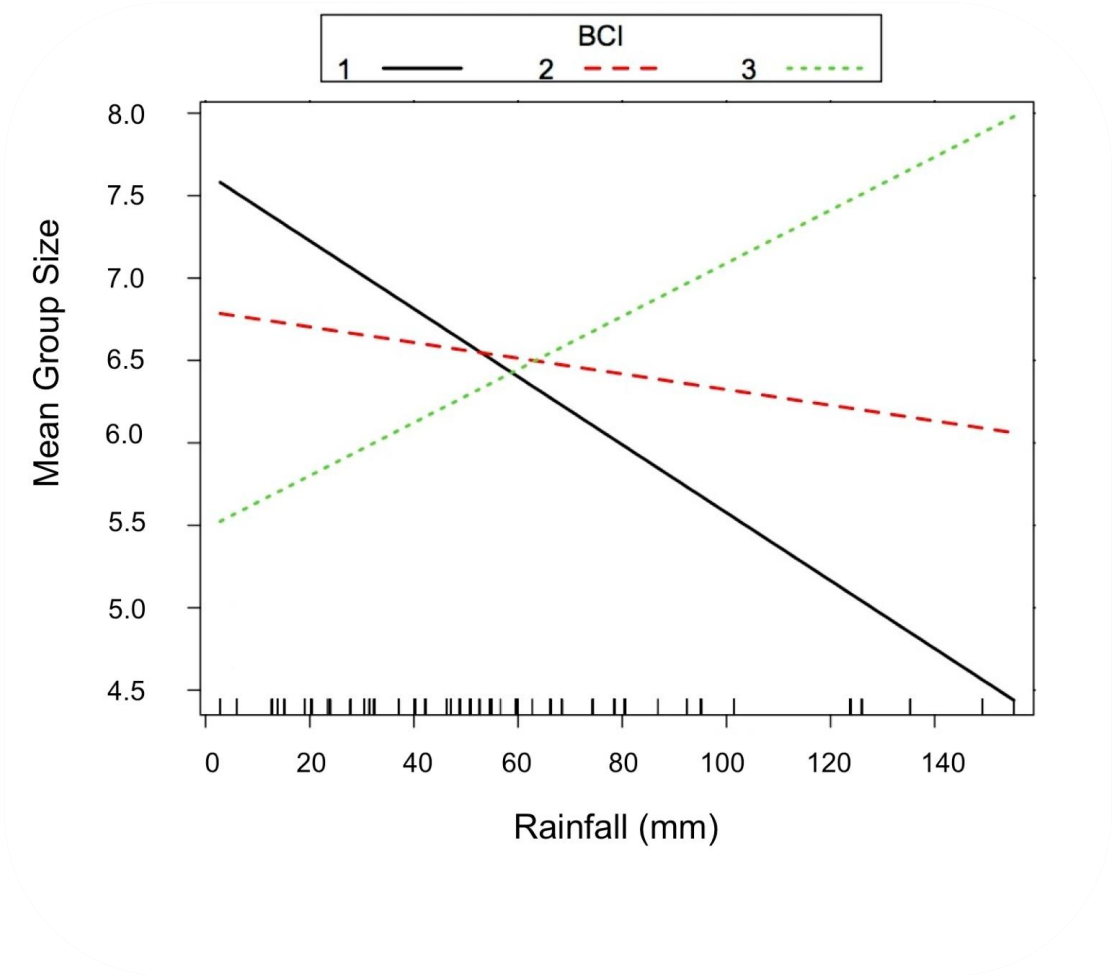

BCI
1
2
3
Mean Group Size
8.0
7.5
7.0
6.5
6.0
5.5
5.0
4.5
0
20
40
60
80
100
120
140
Rainfall (mm)

Figure 3

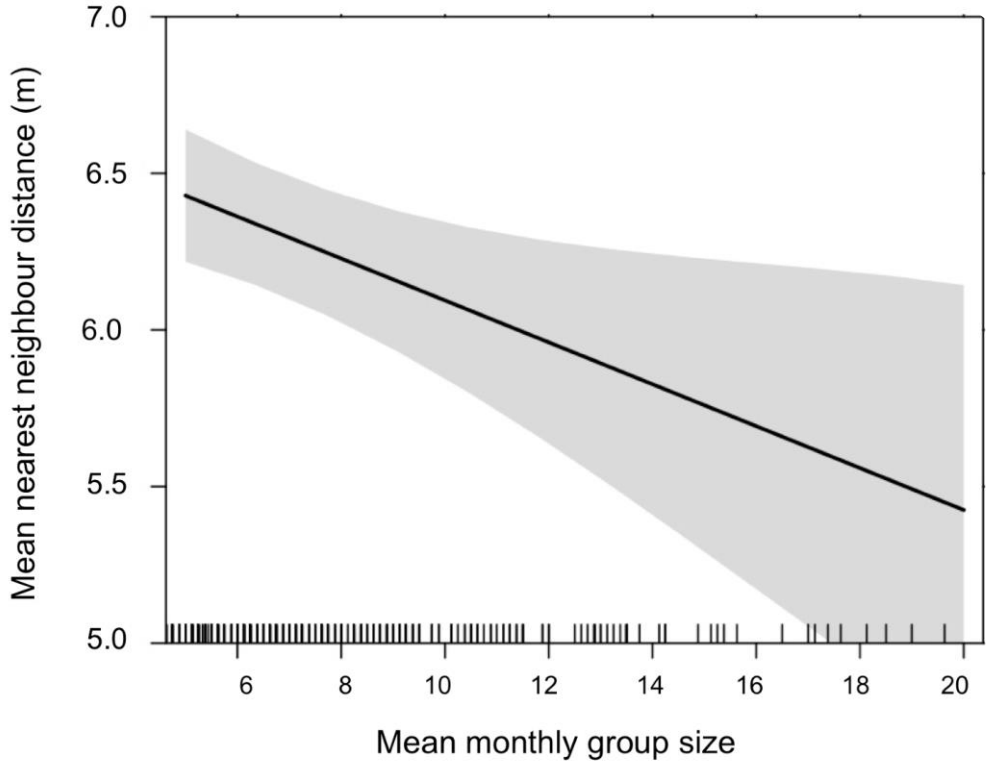

Mean nearest neighbour distance (m)
7.0
6.5
6.0
5.5
5.0
6
8
10
12
14
16
18
20
Mean monthly group size

Figure 4

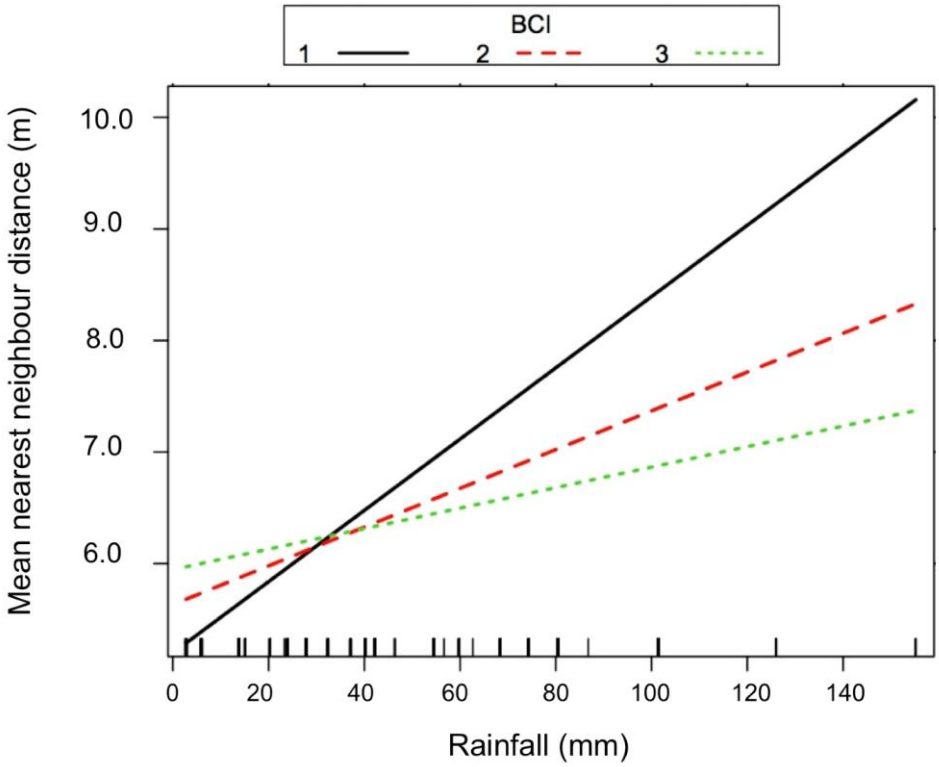
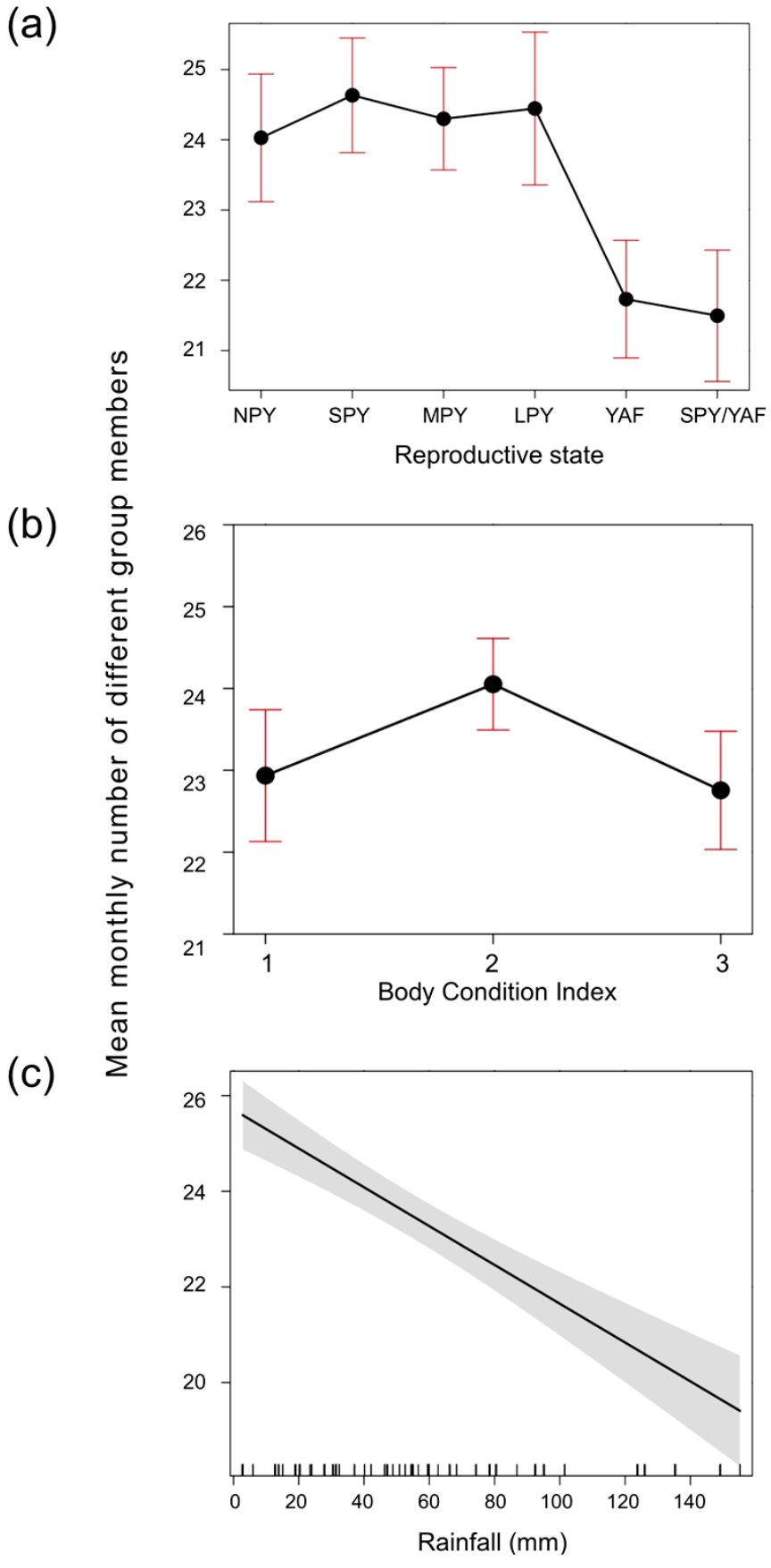

BCI
1
2
3
Mean nearest neighbour distance (m)
10.0
9.0
8.0
7.0
6.0
0
20
40
60
80
100
120
140
Rainfall (mm)

Figure 5


(a)
25
24
23
22
21
NPY
SPY
MPY
LPY
YAF
SPY/YAF
Reproductive state
(b)
Mean monthly number of different group members
26
25
24
23
22
21
1
2
3
Body Condition Index
(c)
26
24
22
20
0
20
40
60
80
100
120
140
Rainfall (mm)

Supplementary material

Table S1: Variance components (with standard deviations) for the random effects of each model

Aim	Female ID (random effect)	Residual variance	Variation explained by random effect
1	0.159 (0.400)	6.606 (2.570)	2.36%
2	0.208 (0.456)	2.725 (1.651)	7.10%
3	2.529 (1.590)	26.846 (5.181)	8.61%
4	0.367 (0.606)	N/A	N/A

Reproductive consequences of individual differences in sociability in a large herbivore

C. Menz, E. Best, N. Freeman, R. Dwyer, S. Blomberg and A. Goldizen

Summary

1. Social integration and close bonds with others is known to improve female reproductive success in some group-living species. However, high levels of sociability can also be costly for individual reproductive success in other species, so the adaptive value of sociability likely depends on multiple variables. Eastern grey kangaroos (*Macropus giganteus*) forage in groups and females demonstrate social preferences amongst their same-sex associates, however the evolutionary significance and fitness consequences of such relationships are unknown.

2. This study examined more than four years of reproductive and social data for females from a population of over 200 individually recognizable wild eastern grey kangaroos, to investigate the reproductive costs and benefits of several facets of sociability. We explored the variables that influenced the reproductive outputs of females over one- and two-year time periods, and those that influenced the survival of known young.

3. Maternal experience was a key factor in reproductive success - primiparous females raised fewer young to pouch emergence and weaning, and the offspring they did produce were less likely to survive. In contrast to expectations, we also found that females with larger social networks produced fewer surviving young than did less sociable females. Females who formed preferential associations with a higher number of other individuals were also less likely to successfully wean their young.

4. The finding that social bonds can be costly for reproductive success in female kangaroos suggests that individuals in our study population may experience a trade-off between successfully rearing young and maintaining social relationships. Social integration may be beneficial for females' survival or other aspects of their fitness under conditions of higher predation risk than was present in the current study. Our results contrast with the notion that social bonds are beneficial for reproductive success, and we suggest that broader ecological conditions be considered when interpreting the fitness consequences of such relationships.

Keywords: Social bonds, kangaroo, social networks, reproductive success, parity, fitness, sociability, predation

Introduction

Living in groups, or sociality, is thought to evolve when the net benefits of associating with conspecifics outweigh the costs (Alexander 1974). Sociality can offer increased protection from predators, opportunities to find mates, and cooperation in obtaining food resources, while its costs include increased intraspecific competition, aggression, and disease transmission (Krause & Ruxton 2002). Among social mammals, the fitness consequences of group size and group composition varies among species, and depends on both intrinsic and environmental factors (Silk 2007; Ebensperger, Rivera & Hayes 2012). Differences in breeding strategy, extent of cooperative behaviour, population density, food abundance, and predation risk are all factors that contribute to this variation, but generally sociality tends confer fitness benefits, including increased reproductive success (Ebensperger, Rivera & Hayes 2012).

Within most mammal social groups, differentiated relationships between members exist, and associations or interactions between individuals are non-random. Close social bonds between kin often constitute the strongest relationships in a group, illustrated in studies on primates (Silk, Seyfarth & Cheney 1999; Silk 2007). The first evidence that close social bonds can benefit individual fitness came from a long-term study of wild savannah baboons (*Papio cynocephalus*), in which females who had close relationships, and were more socially integrated within their group, experienced greater infant survival (Silk, Alberts & Altmann 2003). Positive relationships between individuals' social connections (both direct and indirect) and female reproductive success have since been reported in other primates, including chacma baboons (*Papio cynocephalus ursinus*) (Silk et al. 2009), mandrills *(Mandrillus sphinx*) (Charpentier *et al*. 2012), and rhesus macaques (*Macaca mulatta*) (Brent *et al*. 2013). Among non-primates, strong social integration between non-kin female wild horses (*Equus caballus*) increased the birth rates and survival of foals (Cameron, Setsaas & Linklater 2009). A similar benefit of social bonds in the absence of genetic relatedness was found for bottlenose dolphins (*Tursiops* sp.), where the reproductive fitness of a female's non-kin preferred associates was the strongest predictor of her own calving success (Frère *et al*. 2010a). Although the mechanisms by which social bonds confer fitness benefits are not known for all these species, social bonds (maintained by grooming and other affiliative interactions) can reduce stress hormone levels in female primates (Crockford *et al*. 2008; Wittig *et al*. 2008; Brent *et al*. 2011). Strong female-female social bonds also potentially buffer against male harassment (Cameron, Setsaas & Linklater 2009).

In contrast to these findings, other studies on non-primate mammals have found that social integration can reduce individuals' reproductive success. In yellow-bellied marmots (*Marmota flaviventris*), mammals which live in matrilineal colonies, females with higher affiliation strengths with conspecifics weaned fewer offspring over a year (Wey & Blumstein 2012). The researchers suggested that the consequences of sociability may be density-dependent, with older females suppressing their daughters' reproduction in high density populations (Armitage 1991; Armitage 2012). A similar finding came from research on the red-necked wallaby (*Macropus rufogriseus*), where a negative relationship was found between the gregariousness of a mother and the survival of her young. Here, strong post-weaning associations with previous offspring were also linked to lower infant survival (Johnson 1986). Given these contrasting fitness outcomes for highly sociable individuals in different species, it is likely that interactions with other factors, such as population density and availability of resources, can influence whether close social relationships are beneficial or costly for individuals' fitness.

Although social bonds are most obvious among species that live in stable groups, long-term and non-random relationships between individuals are not restricted to groups with cohesive membership. Populations with frequent changes in groups' spatial cohesion, memberships and compositions are said to demonstrate 'higher fission-fusion dynamics' (Aureli *et al*. 2008). In such species, social connections among kin often contribute to association patterns in a population (especially in species with female philopatry), but the correlation between genetic relatedness and association can be quite weak (Frère *et al*. 2010b; Carter *et al*. 2013b; Best *et al*. 2014). Overlap in space use generally explains much variation in association patterns (Chaverri, Gamba-Rios & Kunz 2007; Carter *et al*. 2013b; Pinter-Wollman *et al*. 2013; Best *et al*. 2014). However, individuals may have strong associations with conspecifics with which they have little home range overlap, or may associate minimally with others with which they have complete home range overlap (Frère *et al*. 2010b; Best *et al*. 2014; Strickland *et al*. 2014). Close and long-term associations between individuals as a component of high fission-fusion dynamics have been described in a number of different taxa, including several bats (Kerth & Köing 1999; Patriquin *et al*. 2010; Kerth, Perony & Schweitzer 2011), Grévy's zebra (*Equus grevyi*) (Sundaresan *et al*. 2007), chimpanzees (*Pan troglodytes*) (Langergraber, Mitani & Vigilant 2009), bottlenose dolphins (*Tursiops* sp.) (Frère *et al*. 2010b) and giraffe (*Giraffa camelopardalis*) (Carter *et al*. 2013a). Several of these species exhibit complex cooperative interactions such as reciprocal grooming, alliance formation or communal care of young, participation in which could increase an individual's fitness. However, as these cooperative behaviours are not present in all of the species mentioned above, close

associations between individuals may provide other adaptive benefits, for example access to resources or protection from predators.

In this study, we explored the fitness consequences of individual differences in sociability in the eastern grey kangaroo (*Macropus giganteus*), a large-bodied grazing macropod which is among the most gregarious of the kangaroos (Kaufmann 1975). Individuals aggregate in temporary foraging groups that frequently change in size and composition (Southwell 1984), although populations can contain communities that remain socially distinct despite some degree of spatial overlap (Jaremovic & Croft 1991; Best *et al*. 2013). Associations among females are non-random, and some females form significantly closer or weaker associations with other females than expected based on spatial overlap alone (Carter *et al*. 2009; Best *et al*. 2014). Although weak genetic structure has been reported in more than one study population (Best *et al*. 2014; King, Garant & Festa-Bianchet 2015), and some sub-adult females continue to associate with their mothers after weaning (Grant 1973; Stuart-Dick & Higginbotton 1989; Jarman 1994), associations among females are correlated less strongly with biparental relatedness than they are with space use (Best *et al*. 2014) – hence, associations between unrelated females are likely to form the majority of the pairwise relationships observed (Best *et al*. 2014). In this study we use data from over four years of study of social grouping patterns and reproductive records from a population of over 200 female kangaroos to investigate the whether there is a relationship between individuals' sociability traits and their reproductive success. We predicted that females exhibiting greater social integration and/or stronger social bonds with other females would reproduce more frequently and/or more successfully than less sociable females. Our study is the first to quantify the fitness correlates of multiple dimensions of female sociability in the wild, in a gregarious mammal with higher fission-fusion grouping dynamics yet without complex cooperative interactions. If social integration is found to relate to reproductive success, fitness benefits could help explain the evolution of social bonds in mammals.

We investigated the relationships between female reproductive success and sociability using three different approaches, designed to incorporate social measures and environmental variables calculated over different time periods (ranging from one month to two years) to allow the influences of a range of factors to be tested. Quantification of individuals' sociability relied on both social network analysis (SNA) methods (Wey *et al*. 2008; Sih, Hanser & McHugh 2009) and non-network measures. Our first approach investigated the factors related to the number of surviving offspring a female produced in a given year. In the second approach, we tested how variables affected the number of offspring a female produced using a longer time scale of overlapping two-year periods. This longer time period allowed us to control for home range overlap when quantifying individuals'

social preferences. As both of these approaches required long-term data, it was not possible to include females' body conditions or monthly rainfall, which fluctuated over short time scales. We therefore used a third analysis to incorporate the influences of these variables on reproductive success, in which we recorded the survival of all known young born during the study period, and explored the environmental and social factors that best explained these survival patterns.

Methods

Field data collection

Field observations were conducted between January 2010 and September 2014 at Sundown National Park in Queensland, Australia (28°55'03''S, 151°34'46''E). The study site spanned 37.4 ha of a patchwork of pasture and eucalypt woodland, bordered on all sides by forest (see Best *et al*. (2013) for a detailed description). The eastern grey kangaroos (referred to hereafter as 'kangaroos') that inhabited the site have been studied by our research group since 2009. An estimated 300 kangaroos grazed regularly within the site during the period of study, including approximately 240 females in any given year. Female kangaroos were individually identified based on their natural features and markings (Jarman *et al*. 1989; Carter *et al*. 2009; Best *et al*. 2013). An extensive catalogue of photographs of each female kangaroo was kept to assist with identifications. Animals that were not immediately recognized in the field were photographed for later comparison to known animals in the database. To ensure consistency of inter-observer identification of animals, all researchers collected fecal samples from animals that were difficult to distinguish in the field to compare DNA genotypes (genetic work described in detail by Best *et al*. (2013), and here in Supplementary Material).

Social association data were collected as described by Best et al. (2013). Each month between 10 and 16 surveys were conducted within the study site in the two hours following sunrise or the two hours prior to sunset. From January 2010 until September 2012, and from January 2014 until September 2014, surveys were conducted once a day, alternating between mornings and evenings. Between October 2012 and December 2013, surveys were conducted either once a day or twice a day (once in the morning and once in the evening). Because temporary foraging groups changed composition almost continuously and broke up during the kangaroos' midday rest period, morning and afternoon surveys were considered independent samples (Carter *et al*. 2009). In each survey, a researcher walked through the site following varied routes with data collected on each group of kangaroos encountered. A group was observed until all female group members were identified. The 15 metre chain rule (i.e. if an individual was within 15 m of another group member they were

included in the group (Jarman 1987)), was used to assign common group membership in female kangaroos. Female kangaroos have been previously observed to maintain social and spatial cohesion at this distance (Favreau, Goldizen & Pays 2010). All members in a group were considered to be associating according to the gambit-of-the-group method (Whitehead & Dufault 1999). Estimates of group size included all adult and sub-adult females within a group, but did not include males of any age. This was done because mature adult males frequently moved among groups of females searching for mating opportunities, and sub-adult males most often grouped with other males of similar size and age classes (Best *et al*. 2013). The distance in metres between each female in the group and her nearest female neighbour was estimated and recorded. The location of the center of the group (or, where possible, the approximate location of each group member) was recorded using a Garmin eTrex H GPS (Garmin International Inc., Olathe, KS, USA). During field sessions in which surveys were not being conducted, GPS locations were taken for females *ad libitum* from 2010 until mid-2012. Until September 2012, survey data were recorded with pen and paper; subsequent survey data were recorded on a Juno 3B Handheld rugged outdoor computer (Trimble Navigation Limited, Sunnyvale, CA, USA).

The reproductive state of female kangaroos was assessed visually based on the presence and developmental stage of their young. Kangaroos give birth after 36 days of gestation to a tiny, blind, and hairless young which then continues its development inside the mother's pouch (Poole 1983). Young are permanently excluded from the pouch (PEP) at approximately 46 weeks after birth, although they begin to leave the pouch on temporary excursions approximately 1-2 months prior to PEP. Young continue to nurse for another seven months on average before they are weaned (Lee & Ward 1989). We recorded the reproductive state of each female encountered during association surveys as one of six categories, as outlined by Best *et al*. (2013): females with no visible pouch-young (NPY), females with a small pouch-young (SPY), females with a medium pouch-young (MPY), females with a large pouch-young (LPY), females with a young-at-foot (YAF) (young that had reached PEP but continued to nurse and remain close to its mother), and females with both a small pouch-young and a young-at-foot (SPY,YAF). Offspring that were independent from their mothers (weaned) but too young to breed were recorded as sub-adults.

Females' body conditions were recorded each month using a modified version of the body condition index (BCI) based on the degree of protrusion of hips and ribs (Best, Blomberg & Goldizen 2015). BCI were distributed into three categories: 1 (poor), 2 (average) or 3 (good, which included Best et al.'s categories 3 and 4). Data on monthly rainfall (in ml) were taken from the Bureau of Meteorology website for Texas Post Office (station number 041100, 28°51'00" S,

151°10'12" E; located approximately 40 km west of the study site). Rainfall varied dramatically over the four-year study period (with a high of 148.5 ml in December 2010 to a low of 1.4 ml in August 2012). Total rainfall for the years 2010 - 2013 (874.3 ml, 689.8 ml, 617.9 ml, and 684.8 ml, respectively) exceeded the average yearly total rainfall for the previous five years (2005- 2009; mean= 614.3 ml/y ± standard error 45.1ml).

Data analysis - Approach 1

The first approach used annual association survey data and reproductive records collected between January and December across the four survey years. Only females of reproductive age that were recorded on association surveys at least ten times in a year were included in the analyses. To reduce the possibility of missing reproductive milestones in less-frequently seen animals, the data set was further restricted to only those females whose reproductive state had been recorded at least once every two months. One hundred and twenty-six individual females met these criteria for inclusion in the analyses, with a total of 285 female-year sample points recorded (N = 68 (2010), 78 (2011), 59 (2012) and 80 (2013)). For each female in a given year, the number of young she produced that survived to the LPY stage and to PEP was recorded, as was whether the female weaned a young in that year. Based on past reproductive states and/or previous offspring, the parity of most females was known. Where prior reproduction was unknown, individuals' parity status for that year was recorded as absent.

Individuals' measures of sociability were calculated using the program SOCPROG2.4 (Whitehead 2009). For each year, association survey data were used to generate a matrix of pairwise association indices between all individuals in the population. The half-weight index (HWI) was used as the association index (Cairns & Schwager 1987), calculated using the formula HWI = $N_{ab}/0.5(N_a/N_b)$, where N_{ab} is the number of sampling periods where individuals A and B were observed associating, N_a is the number of sampling periods where A was observed, and N_b is the number of sampling periods where B was observed. The HWI matrix was then used to calculate the following five social network measures for each individual: Strength, the sum of association indices for an individual; Eigenvector Centrality, a measure of an individual's connectedness within the network; Reach, the overall strength of an individual and its neighbours; Clustering Coefficient, a measure of how well connected an individual's neighbours were amongst themselves; and Affinity, the weighted mean strength of an individual's neighbours (Whitehead 2008).

A principal components analysis was used to reduce the number of these social network variables (Table S1, Supplementary Material). This and all subsequent analyses were conducted in the R Programming Language (R Core Team 2013). The first two principal components (hereafter termed Soc1 and Soc2) explained 74% and 16% of the variation in the data, respectively, and scores were calculated for these components for each individual in each year. All five social network metrics loaded negatively onto Soc1, with loadings of close to -0.50 for the measures Strength, Reach, and Affinity, which suggested that this component reflected the size of an individual's social network, or number of connections. Soc2 had loadings of 0.74 for Eigenvector Centrality and -0.65 for Clustering Coefficient. Both of these latter measures quantify aspects of how an individual is indirectly connected to others in the network, hence Soc2 was considered to reflect the arrangement of connections in an individual's network. Since the majority of the strong loadings of variables onto the components were negative, individuals' scores were multiplied by negative one for ease of interpretation – thus positive scores for Soc1 represented higher scores on the component social network values. As a non-network measure of sociability, the average group size in which a female was encountered during surveys in a year was calculated.

These reproductive and social data were analysed using three generalized linear mixed models. The first two models compared survival of LPY (model 1) and PEP (model 2), using count data as the response variable (0, 1, or 2 offspring produced that survived to this stage). The third model investigated the probability producing a young that survived to weaning, using the success of weaning as a binomial response variable (no female weaned more than one young per year). In all models, female ID was included as a random effect, and the explanatory variables were individuals' scores on Soc1 and Soc2, mean annual group size, number of recordings on surveys, whether a female was primiparous, and survey year. Colinearity among the explanatory variables was checked by calculating variance inflation factors (VIFs) from the raw data. None of the variables had VIF values > 4, indicating an acceptable degree of colinearity.

Data analysis - Approach 2

In the second approach, association survey data were distributed into three overlapping two-year periods: (Jan 2010 - Dec 2011 (Period A), Jan 2011 - Dec 2012 (Period B), and Jan 2012 - Dec 2013 (Period C). Data were included for only those reproductively mature females who had been recorded in association surveys at least ten times in a given two-year period, and also had a minimum of 50 GPS location fixes. This resulted in sample of sizes of 87, 78, and 79 females for time periods A, B, and C respectively (total = 244 female/time periods with 110 different individuals). Association survey data were entered into SOCPROG2.4 for each two-year period to

generate the five described social network measures for each female kangaroo. A principal components analysis was then conducted on these five network measures (Supplementary Material, Table S2). The first two components PC1 and PC2 explained 75% and 17% of the variance, respectively. All five social network measures had positive loadings onto PC1 of 0.34 or higher, with Strength, Reach and Affinity loading at approximately 0.50. This component was considered to represent measures of social network size. Eigenvector Centrality loaded negatively onto PC2 at -0.76, while Clustering Coefficient loaded positively onto this component at 0.61, so this component likely encapsulated the arrangement of direct and indirect ties within an individual's social network. Scores for these two variables for each of the 244 female/time periods were generated for use as explanatory variables in subsequent analyses.

An additional measure of longer-term social patterns was included in these analyses, which characterized dyadic associations between females that were stronger than expected by pair-wise home range overlap alone. This was done following the method outlined by Best *et al*. (2014), using the DigiRoo2 software package in R (Dwyer, Best & Goldizen 2013), which randomizes association survey data based on individuals' space use in order to create a null model for pair-wise associations. As specified previously, in each time period only females with 50 or more GPS location points were included, as this was the minimum number of points needed to obtain accurate home range estimates (Best *et al*. 2014). From these spatial data, two hundred simulated surveys were generated based on parameters from observed surveys, and these were entered into SOCPROG2.4 to generate expected association indices for all dyads based on individuals' space use, controlling for individual differences in gregariousness by using a variation on the half-weight index (known as HWIG, see Godde *et al*. 2013) as the association index. The expected association indices for each dyad were then compared to the observed association index. If the observed association index was in the top 2.5% of expected values, the pair was categorized as preferred associates, and if the observed association index was in the bottom 2.5% of expected values, the pair was classed as avoided associates (Best *et al*. 2014). If an observed association index fell between these extremes, the relationship was classed as casual. The total number of preferred associates that each female had over a two-year period was then taken as a non-network measure of individual sociability.

To test the relationship between sociability and three stages of young survival (survival to LPY, survival to PEP, and survival to weaning), linear mixed models fitted by maximum likelihood were constructed in R. Here, the response variable was whether or not a female produced a young that survived to the stage in question during the second year of a two-year time period. Social

explanatory variables included a female's mean group size, number of preferred associates, and PC1 and PC2 scores. Other variables were: whether a female was primiparous or not, and the number of times each female had been recorded on surveys during the two years. The explanatory variables were checked for colinearity prior to running the model, and two of the variables (PC1 and Time Period) were found to have VIF values greater than 4 (square root of VIF > 2). However, since the social network measures contributing to PC1 varied among Time Periods A, B, and C (data not shown), this relationship between the variables was expected, and both variables were retained in order to control for the differences in PC1 between time periods.

Data analysis- Approach 3

A third approach was used to explore if short-term social and environmental variables influenced the survival of offspring. Data sets included each known young born in the population, and whether it survived to each of three developmental stages (LPY, PEP, and weaning). For each young we included an environmental variable (rainfall in mm), body condition index of the mother (1 - 3), and measures of the mother's sociability, over specified periods of time (described below). Only young that lived to be large enough for their presence in the pouch to be evident were included in the analysis. Such pouch distention was observable in the field when a young was approximately three months old, when it would have weighed over 100 g and had a tail length of approximately 80 mm (Poole et al. 1982).

The first analysis included all young observed at the SPY stage, and recorded whether each of these young survived to the LPY stage or not, and the month in which they were first recorded at this stage. For the young that did not survive to LPY, their projected month of reaching LPY was determined based on the average time of 8.4 months (standard deviation = 1.3 months) between first sighting as a SPY and reaching the LPY stage for known surviving offspring (N = 138). Data for explanatory variables were taken from various points during this time period, described below and in detail in Table S3 (Supplementary Material). The BCI score of the mother was taken from the month in which her young was first recorded as a LPY. We excluded data from mothers that were recorded on association surveys infrequently during their young's pouch development, with only the offspring from females observed fifteen or more times during the seven months prior to the offspring reaching the LPY stage included in the analyses. Lagged rainfall (by one month) was used as a proxy for the availability of grass, which responded rapidly to rain in the study area (this thesis, Chapter 4). Total rainfall (recorded at the Texas BOM Station) during the three months prior to the young reaching LPY stage was summed. Where known, it was recorded whether the young's mother was primiparous or not. It was not feasible to use social network metrics or pairwise

association indices to quantify mothers' sociability, as these measures rely on longer-term data. Instead, as measures of individuals' sociability we used females' mean foraging group sizes, and females' mean distances to their nearest neighbours while foraging. These measures were averaged over the three-month period prior to an individual's young reaching LPY stage.

The second analysis included all young known to have survived to LPY, and recorded whether each of these young survived to PEP or not. Explanatory variables were the same as were used in the first analysis (Table S3, Supplementary Material), as was the minimum number of times a female needed to be observed (i.e. fifteen) to include her young in the analysis. Finally, a third analysis included the young that survived to PEP and recorded whether or not they survived to weaning. Similarly to the previous analyses described above, in this analysis we also used data on rainfall, mothers' social measures, and mothers' body conditions. However, these measures were calculated over different time periods to the previous two analyses, in order to incorporate data from both before and after the young reached PEP. Rainfall was recorded over the three months prior to the young's month of PEP, while mothers' BCIs from the month in which her young reached PEP were used. Mothers' mean group sizes and nearest neighbour distances were averaged over the month of PEP and the two months that followed, while the number of times females were observed on surveys was counted for the month of PEP plus six additional months. These time periods are also shown in Table S3 (Supplementary Material). In this analysis, we included only females observed ten or more times during this period of weaning.

Generalized linear mixed-effects models were fitted for each of these three datasets, using survival of young to the developmental stage of interest as the response variable. Rainfall, along with mothers' BCI scores, mean group sizes, mean nearest neighbour distances, and numbers of observations were included as explanatory variables. None of the explanatory variables in any of the models had VIFs > 4. Female ID was included as a random effect in each model.

Results

Approach 1

Primiparous females produced fewer offspring that survived to large pouch-young stage than multiparous females did on a 12-month time scale (Table 1a), and no other explanatory variables were significant. Primiparous females also tended to produce fewer offspring that survived to PEP,

although this was not significant (Table 1b). There was also a non-significant trend for females with high scores on the Soc1 PCA component to produce fewer young that survived to PEP.

Females were significantly more likely to raise a young to weaning in 2011, 2012 and 2013 than in 2010 (Table 1c), and individuals recorded on more surveys were also significantly more likely to be known to have weaned a young. Primiparous females were less likely to wean a young than were multiparous females, as were females scoring highly on Soc1, and both these variables were significant (Figure 1).

Approach 2

Females recorded on more surveys within a two-year period were significantly more likely to have been seen to produce a young that survived to LPY during the second year (Table 2a). The number of observations of a female was also significantly positively related to her producing a young that survived to PEP (Table 2b). Primiparous mothers had a lower probability of producing an offspring that survived to PEP than did multiparous females.

Several variables were significantly related to whether a female weaned a young in the second year of a two-year period. Females observed more frequently were more likely to be known to have weaned a young (Table 2c), and primiparous mothers had a lower probability of producing a young that survived to weaning than did multiparous females. Of the variables related to individual sociability, females with a greater number of preferred associates were less likely to wean a young than females with fewer preferred associates (Figure 3).

Approach 3

When examining the survival of every infant, young born to primiparous mothers were significantly less likely to survive to LPY stage (Table 3a). Young whose mothers were observed more frequently during the young's pouch development were more likely to have been known to survive to the LPY stage, although the number of observations of a mother was not related to the survival of her young to later developmental stages. The offspring of primiparous mothers were also less likely to survive to PEP (Table 3b). Higher rainfall during the final months of a young's pouch development increased the likelihood that the young would survive to PEP.

Two explanatory variables significantly predicted survival of young from PEP to weaning. Mothers that foraged at a greater mean distance from their nearest group-mate were more likely to successfully wean their young (Table 3c) (Figure 3). Rainfall was also positively related to offspring survival to weaning. There was no significant effect of maternal experience on a young's likelihood of surviving to weaning. Neither the mean group sizes in which females were encountered, nor females' body condition indices, were significantly related to survival of their young at any developmental stage in this set of models.

Discussion

In group-living species, the nature and quality of an individual's relationships with others may contribute towards its fitness. We analysed a multi-year dataset using several approaches to explore the factors contributed to offspring survival, and thus females' reproductive success, in wild eastern grey kangaroos. Our results show that in addition to maternal experience and environmental conditions, patterns of sociability affected both the number of offspring females produced and the probability of their offspring surviving.

The variables that influence the survival of a young may change throughout its development. A study on wild crested macaques (*Macaca nigra*) showed that the determinants of offspring survival, including those related to the mother's social environment, are different at the fetal and the infant stages of development (Kerhoas *et al*. 2014). Marsupials have short gestation periods compared to eutherians, but infancy can be similarly separated into pouch development and post-pouch development. However, young also undergo an 'in-and-out' of the pouch phase between these period, lasting approximately five weeks in the eastern grey kangaroo (Poole 1975), in which they can experience the same risks as young that are permanently excluded from the pouch (PEP). Our study examined three stages of development: birth to large pouch-young (LPY) stage, large pouch-young stage to PEP, and PEP to weaning. We found the seven-month period between PEP and weaning is when mother's level of sociability has the greatest influence on her offspring's survival. Several aspects of sociability influenced whether a female weaned a young over a one- or two-year period, and whether a PEP young would survive to weaning. Although survival of young to earlier developmental stages of LPY and PEP was also predicted by several variables – numbers of observations, rainfall, and maternal experience – we did not find a significant influence of individual sociability at these stages.

In contrast to recent studies of group-living mammals that have reported fitness benefits of sociability in females (Cameron, Setsaas & Linklater 2009; Silk *et al*. 2009; Frère *et al*. 2010a), we found a negative relationships between individual sociability and reproductive success across a number of social network measures and temporal scales. Females with larger social networks (signified by scores based on principal components analysis) were less likely to wean a young in a given year. When considering measures of sociability over a two-year time interval, social network measures were not related to reproductive output. However, females with more preferential associations within the population were less likely to wean young. The average group size in which a female was observed was not a significant predictor of offspring survival for any developmental stage, further suggesting that the number of individuals within a foraging group is of less importance than the identities of these individuals. A third analysis examining the survival of each young did not consider the identities of a females' associates, but showed that another aspect of social behaviour can influence offspring survival, when controlling for average foraging group size. Following permanent emergence from the pouch, the offspring of females which foraged at greater distances from their nearest group-mate were more likely to survive to weaning. Surprisingly, female body condition did not influence whether young survived to any of the developmental stages tested, although maternal body weight or condition has been found to relate to female reproductive success in ungulates (Festa- Bianchet, Gaillard & Jorgenson 1998; Côté & Festa-Bianchet 2001).

Although larger group sizes can relate to lower direct fitness for individual females in certain species and ecological contexts (Ebensperger, Rivera & Hayes 2012), fewer studies have found a relationship between other measures of individual sociability and reduced reproductive success. Wey and Blumstein (2012) found lower annual reproductive success for female yellow-bellied marmots with high social affiliation strength. They suggested that negative effects of population density could help explain this finding, given that marmots are colonial animals that can experience a high degree of social competition for food and burrows (Armitage 1991). Lower reproductive success was also reported in more gregarious female red-necked wallabies, although this was only significant for an individual's gregariousness within her own matrilineal group (Johnson 1986). Competition for food with closely related associates was proposed as an explanation for the lowered reproductive success of more social wallabies. Female mammals tend to be more socially tolerant of kin than of non-kin (Clutton-Brock & Huchard 2013), and one study reported that female kangaroos are less frequently aggressive towards kin than towards non-relatives when approached closely (Jarman 1994). This suggests that under circumstances where food is patchily distributed, individuals that have strong associations with others may also experience the cost of increased food competition with these associates. The extent to which associations among female kin help shape

broader patterns of gregariousness in kangaroos is not well known (but see Best *et al*. 2014). Future studies examining the fitness consequences of sociability could this relationship to determine if costs to reproductive success are related to competing with relatives for resources.

The inverse relationship between post-PEP young survival and female sociability found in our study may be a result of an increased likelihood of a young becoming separated from its mother. Although a female's mean group size was not significantly related to offspring survival, the density of animals within temporary foraging groups may be. Young-at-foot (YAF) often follow females that were not their mothers upon group fission (C. Menz and N. Freeman, pers. obs.), and in higher-density groups it would be more likely that a young may mistake another animal for its mother and become separated from its mother after it follows this unrelated female. The capacity to recognize kin has been reported in at least one other macropod species (Blumstein, Ardron & Evans 2002), and female eastern grey kangaroos can maintain associations with their adult daughters (Jarman 1994). However, the ability to distinguish kin may not be as strong for mothers and their YAF, and swapping of pouch-young between females (likely unintentionally) has been observed in this species (King *et al*. 2015). Females with large social networks, or with a large number of preferred associates, might also have larger foraging ranges in order to maintain social associations with a large number of individuals. A larger foraging range would make less likely that a young would be able to find its mother again if it becomes separated from her, and future work could test this explanation.

It is important to note when interpreting our analyses, however, that our results do not allow us to conclude that a causal relationship exists between a female's pattern of sociability and her reproductive success. Although we have demonstrated an association between high sociability and lower reproductive success, which may indicate that high social integration leads to reduced reproduction, it is also possible that successfully reproducing causes females to become less sociable. These alternate interpretations of this association were also noted by Wey and Blumstein (2012), who reported lower reproductive success among highly sociable female yellow-bellied marmots. Using long-term observational data, such as those analysed in the present study, it is difficult to separate these two possibilities. Although further studies could potentially experimentally manipulate either females' social environments or their reproductive success to untangle this question, but such experiments would obviously be difficult to do on wild kangaroos.

Although we have reported a potential reproductive cost to females being sociable, it is possible that the costs and benefits of sociability vary with environmental conditions (such as food availability and population density), so that the relationship between sociability and reproductive may differ between populations. The possibility also exists that the relatively short time period over which this study was conducted does not reflect the general pattern for female eastern grey kangaroos. Continuing to study the reproductive outputs and social grouping patterns of individuals in our study population over their lifetimes will help to determine the importance of environmental fluctuations in moderating the relationship between reproductive success and sociability. Given that some studies have shown that female kangaroos can benefit from sociality by spending less time engaging in anti-predator vigilance (allowing more time to feed) when foraging in larger groups (Jarman 1987; Favreau, Goldizen & Pays 2010), it seems puzzling that having close relationships with particular other individuals is linked to lower reproductive success. However, social integration may confer other kinds of fitness benefits for adult females, such as increased longevity, that could outweigh the costs of reduced survival of their offspring. Thus, individual differences in sociability may reflect a trade-off between reproduction and survival for adult females. Sociable females from populations under predation pressure could benefit from their social integration in terms of greater survival or longevity, but since our field site lacks predators of adult kangaroos (such as the dingo, *Canis lupus dingo*) we are unable to test this idea.

Higher rainfall during the last months of a young's pouch life significantly increased its chances of surviving to PEP or to weaning, although rainfall did not affect a young's likelihood of surviving prior to reaching the LPY stage. Since the time of a young's pouch emergence is when its mother incurs the highest energetic cost of reproduction (Gélin *et al*. 2013), mothers may abandon their LPY in times of low rainfall because they are unable to cope with the nutritional demands of lactation. The current study was conducted during a period of higher-than-average yearly rainfall for the region, although the availability of grass varied during the four years of study (unpublished data). It is possible that variable long-term patterns of rainfall in which drought and favourable conditions alternate (as were experienced in this study) may moderate the costs and benefits of individual sociability in grazing herbivores.

Reproductive success is known to increase with age (until the onset of reproductive senescence) in many species of mammal, as more experienced females can better protect their young or target their maternal care more effectively (Cameron *et al*. 2000). We have shown that similar patterns of reproductive success occur in eastern grey kangaroos by comparing primiparous and experienced mothers. Both the production and survival to pouch emergence of offspring were lower for primiparous females. The young of primiparous females were just as likely to survive to weaning

after permanent emergence from the pouch, however, as the young of experienced mothers, although the small sample size of primiparous females with young that reached PEP may have biased this result. Primiparous females in our study were aged between 29 and 54 months when they first bred, and the youngest females in this category may not have reached full adult body size by this time (Poole, Carpenter & Wood 1982). It is possible that primiparous mothers with smaller body sizes were more stressed than by the energetic demands of carrying pouch-young than were older mothers, but that all young faced similar levels of threat following PEP (from predation, separation from their mother, etc.). Older mothers might also know from experience the level of maternal care they need to direct to their pouch-young prior to PEP. Experienced mothers may direct more care to their young prior to its emergence from the pouch than first time mothers. It is possible that the lack of success of primiparous females might also be related to environmental conditions or food availability, as this difference was not found between older and younger mothers in a different study population of kangaroos (Stuart-Dick & Higginbotton 1989).

In conclusion, it is likely that female reproductive output and offspring survival in eastern grey kangaroos are influenced by the combination of a number of factors intrinsic and extrinsic to the population, and across populations with different predation pressure. Variation in females' level of social integration contributes to individual differences in reproductive success, as do maternal experience and environmental conditions. Long-term and broad-scale studies in this and other species will offer greater insight into the circumstances under which individual sociability confers an adaptive advantage.

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Figure Legends

Figure 1. Predicted probabilities of a female weaning a young in each of the four years from 2010 - 2013 for a range of Soc1 (sociability) scores, for a) multiparous females, and b) primiparous females. Solid lines represent predicted values, and dashed lines are the 95% confidence intervals surrounding these predictions.

Figure 2. Predicted probabilities of a female weaning a young in the second year of a two-year period for a range of numbers of preferred associates, for a) multiparous females, and b) primiparous females. Solid lines represent predicted values with dashed lines the 95% confidence intervals.

Figure 3. Predicted probabilities of a young surviving to weaning, with increasing average distance of its mother from her nearest neighbour when foraging, for three levels of body condition index (BCI: 1= poor, 2 = average, 3 = good), for a) multiparous females, and b) primiparous females.

Figures and Tables

a)

Parameter	Estimate	Std. error	z-value	p-value
(Intercept)	-0.2529	0.1392	-1.817	0.0691
Year2011	0.0097	0.2100	0.046	0.9632
Year2012	0.1599	0.2124	0.753	0.4514
Year2013	-0.0236	0.2179	-0.108	0.9136
Soc1	-0.0129	0.1029	-0.125	0.9005
Soc2	0.0125	0.0737	0.169	0.8655
# Sightings	0.1089	0.0885	1.230	0.2188
Primiparity	**-0.7677**	**0.3247**	**-2.364**	**0.0181**
Mean group size	-0.1066	0.0985	-1.083	0.2790
Number of observations = 285, Number of females = 126				

b)

Parameter	Estimate	Std. error	z value	p-value
(Intercept)	-0.5055	0.1568	-3.224	0.0013
Year2011	0.0251	0.2278	0.110	0.9123
Year2012	0.2360	0.2394	0.986	0.3242
Year2013	-0.1384	0.2554	-0.542	0.5879
Soc1	-0.2201	0.1243	-1.770	0.0767
Soc2	0.0586	0.0814	0.721	0.4712
# Sightings	0.1471	0.0971	1.515	0.1297
Primiparity	-0.7126	0.3793	-1.879	0.0603
Mean group size	-0.0724	0.1086	-0.667	0.5049
Number of observations =285, Number of females = 126				

c)

Parameter	Estimate	Std. error	z-value	p-value
(Intercept)	-1.1709	0.3531	-3.316	0.0009
Year2011	**1.318**	**0.4841**	**2.723**	**0.0065**
Year2012	**2.5362**	**0.5569**	**4.554**	**5.26E-06**
Year2013	**1.4912**	**0.5237**	**2.848**	**0.0044**
Soc1	**-1.1741**	**0.2857**	**-4.11**	**3.96E-05**
Soc2	0.179	0.1747	1.025	0.3056
# Sightings	**0.9202**	**0.2405**	**3.826**	**0.0001**
Primiparity	**-3.9448**	**1.117**	**-3.532**	**0.0004**
Mean group size	0.207	0.2218	0.934	0.3505
Number of observations = 282, Number of females = 124				

Table 1: Full model output results for *Approach 1* analyses (single years). a) Model output for how many young a female produced in a given year that survive to LPY stage, b) model output for how many young a female produced that survive to PEP, and c) model output for how many young a female weaned. Significant variables are in **bold**.

a)

Parameter	Estimate	Std. error	z-value	p-value
(Intercept)	1.4283	0.9098	1.570	0.1164
Time Period B	-0.1714	1.0270	-0.167	0.8674
Time Period C	0.0205	1.6796	0.012	0.9903
# of sightings	**0.8215**	**0.4109**	**1.999**	**0.0456**
# pref. associates	0.0792	0.3050	0.260	0.7950
Primiparity	-0.9429	0.6022	-1.566	0.1174
Mean group size	-0.1954	0.4199	-0.465	0.6417
PC1	-0.1420	0.7183	-0.198	0.8433
PC2	0.3468	0.4281	0.810	0.4179
Number of observations = 241, Number of females = 110				

b)

Parameter	Estimate	Std. error	z-value	p-value
(Intercept)	0.2438	0.5831	0.418	0.6758
Time Period B	-0.2826	0.6971	-0.405	0.6852
Time Period C	0.3627	1.1486	0.316	0.7522
# of sightings	**0.6249**	**0.2716**	**2.301**	**0.0214**
# pref. associates	-0.1747	0.1889	-0.924	0.3552
Primiparity	**-0.8423**	**0.4301**	**-1.959**	**0.0502**
Mean group size	-0.0200	0.2745	-0.073	0.9420
PC1	-0.5760	0.4990	-1.154	0.2484
PC2	0.3376	0.2780	1.214	0.2246
Number of observations = 241, Number of females = 110				

c)

Parameter	Estimate	Std. error	z-value	p-value
(Intercept)	1.0900	0.7065	1.543	0.1229
Time Period B	-1.2855	0.8210	-1.566	0.1174
Time Period C	-0.4583	1.3631	-0.336	0.7367
# of sightings	**0.8070**	**0.3342**	**2.415**	**0.0157**
# pref. associates	**-0.7373**	**0.2407**	**-3.063**	**0.0022**
Primiparity	**-2.6016**	**0.7011**	**-3.711**	**0.0002**
Mean group size	-0.6348	0.3562	-1.782	0.0747
PC1	-0.2541	0.5946	-0.427	0.6691
PC2	0.4201	0.3207	1.310	0.1902
Number of observations = 235, Number of females =109				

Table 2: Model outputs for *Approach 2* analyses (two-year time periods), using the binary response variable of whether a female produced a young during the second year of a two-year period that survived to the following developmental stages: a) LPY, b) PEP, and c) weaning. Significant variables ($p < 0.05$) are in **bold**.

a)

Parameter	Estimate	Std. error	z-value	p-value
(Intercept)	0.9094	0.3965	2.293	0.0218
Primiparity	**-1.3510**	**0.5631**	**-2.399**	**0.0164**
NN distance	0.0359	0.2076	0.173	0.8627
Rainfall	0.0780	0.2719	0.287	0.7742
BCI 2	0.7369	0.5031	1.465	0.1430
BCI 3	0.5749	0.5924	0.970	0.3318
Mean group size	-0.1962	0.1814	-1.082	0.2794
# of sightings	**0.4865**	**0.2198**	**2.214**	**0.0268**
Number of observations = 175, Number of females = 82				

b)

Parameter	Estimate	Std. error	z value	p-value
(Intercept)	1.0023	0.4643	2.159	0.0309
Primiparity	**-1.4931**	**0.6911**	**-2.161**	**0.0307**
NN distance	-0.1698	0.2146	-0.792	0.4287
Rainfall	**0.6785**	**0.3125**	**2.172**	**0.0299**
BCI 2	0.2566	0.5165	0.497	0.6194
BCI 3	0.8797	0.7108	1.238	0.2158
Mean group size	-0.2614	0.1892	-1.382	0.1671
# of sightings	0.1406	0.2209	0.637	0.5243
Number of observations = 135, Number of females = 67				

c)

Parameter	Estimate	Std. error	z-value	p-value
(Intercept)	2.6362	0.8522	3.094	0.0020
Primiparity	-2.0145	1.3357	-1.508	0.1315
NN Distance	**0.9577**	**0.4080**	**2.347**	**0.0189**
BCI 2	1.0238	0.6887	1.486	0.1371
BCI 3	0.1212	0.9327	0.130	0.8966
Rainfall	**2.1257**	**0.6821**	**3.116**	**0.0018**
Mean group size	-0.2423	0.2675	-0.906	0.3652
# of sightings	0.3358	0.4122	0.815	0.4153
Number of observations = 99, Number of females = 55				

Table 3: Full model output results from *Approach 3* analyses (survival of each known young), using the binary response variable of survival/non-survival to: a) LPY, b) PEP, and c) weaning. Significant variables ($p < 0.05$) are shown in **bold**.

Figure 1

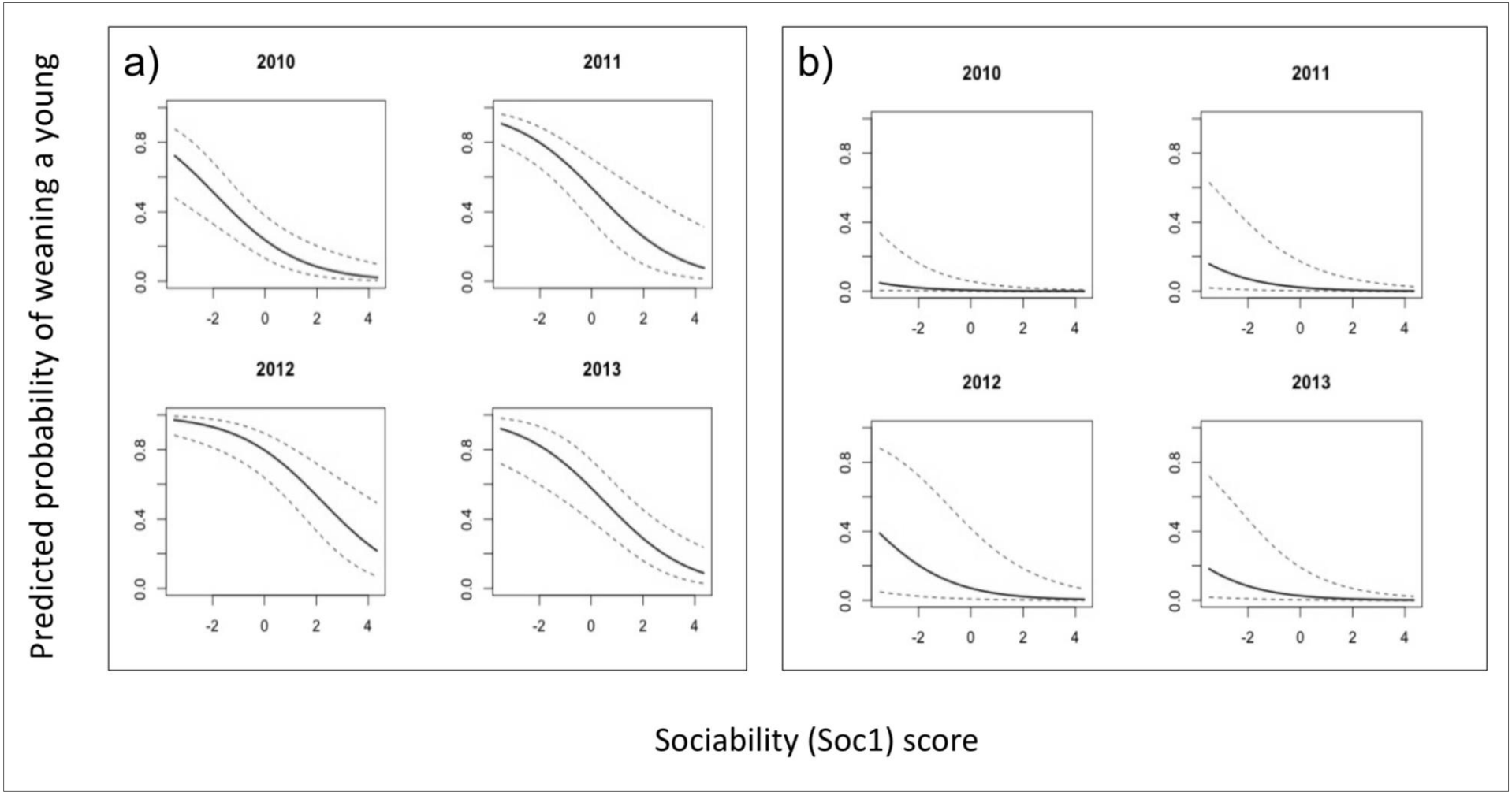

a)
2010
2011
2012
2013
b)
2010
2011
2012
2013
Predicted probability of weaning a young
Sociability (Soc1) score

Figure 2

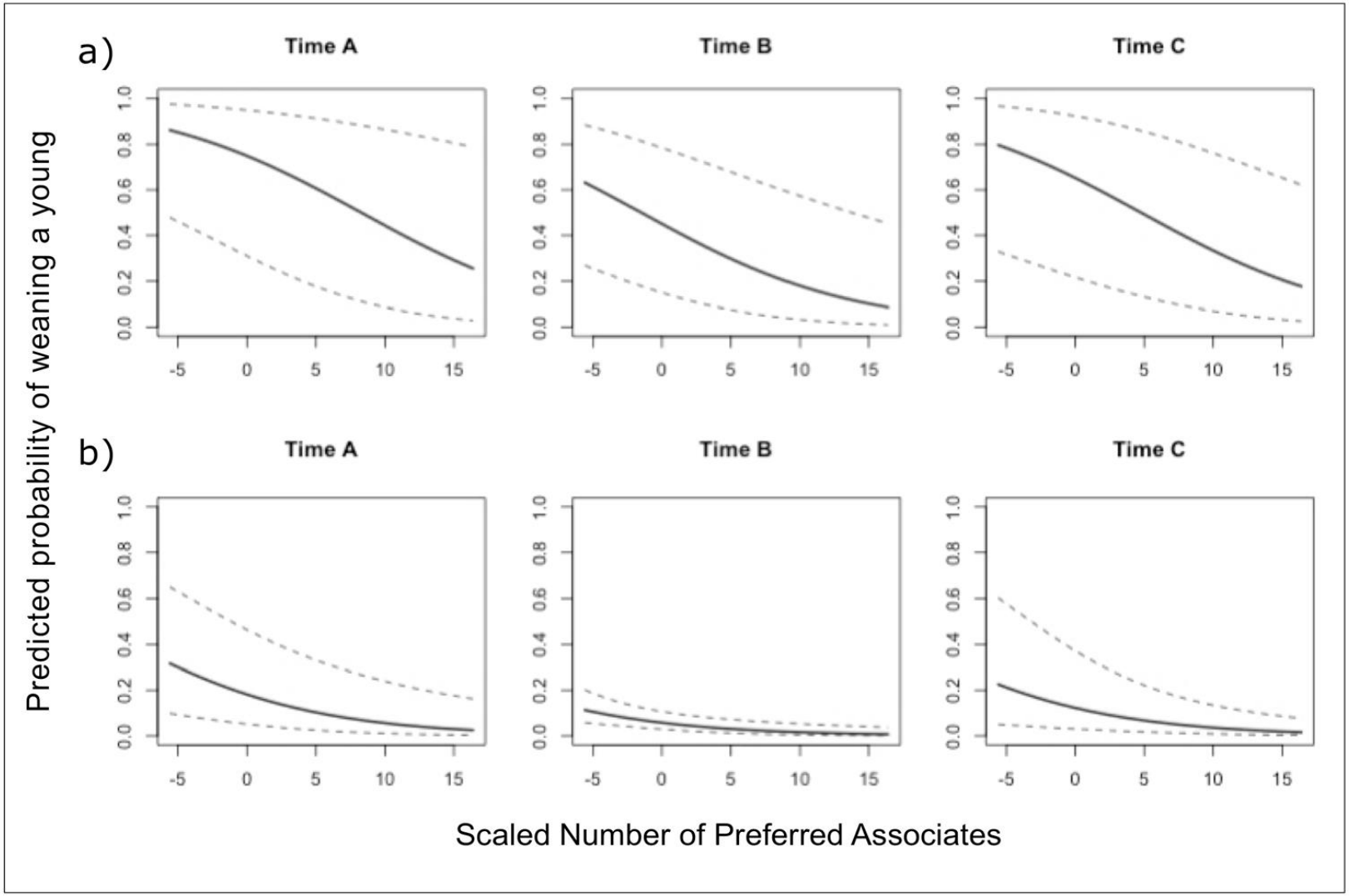
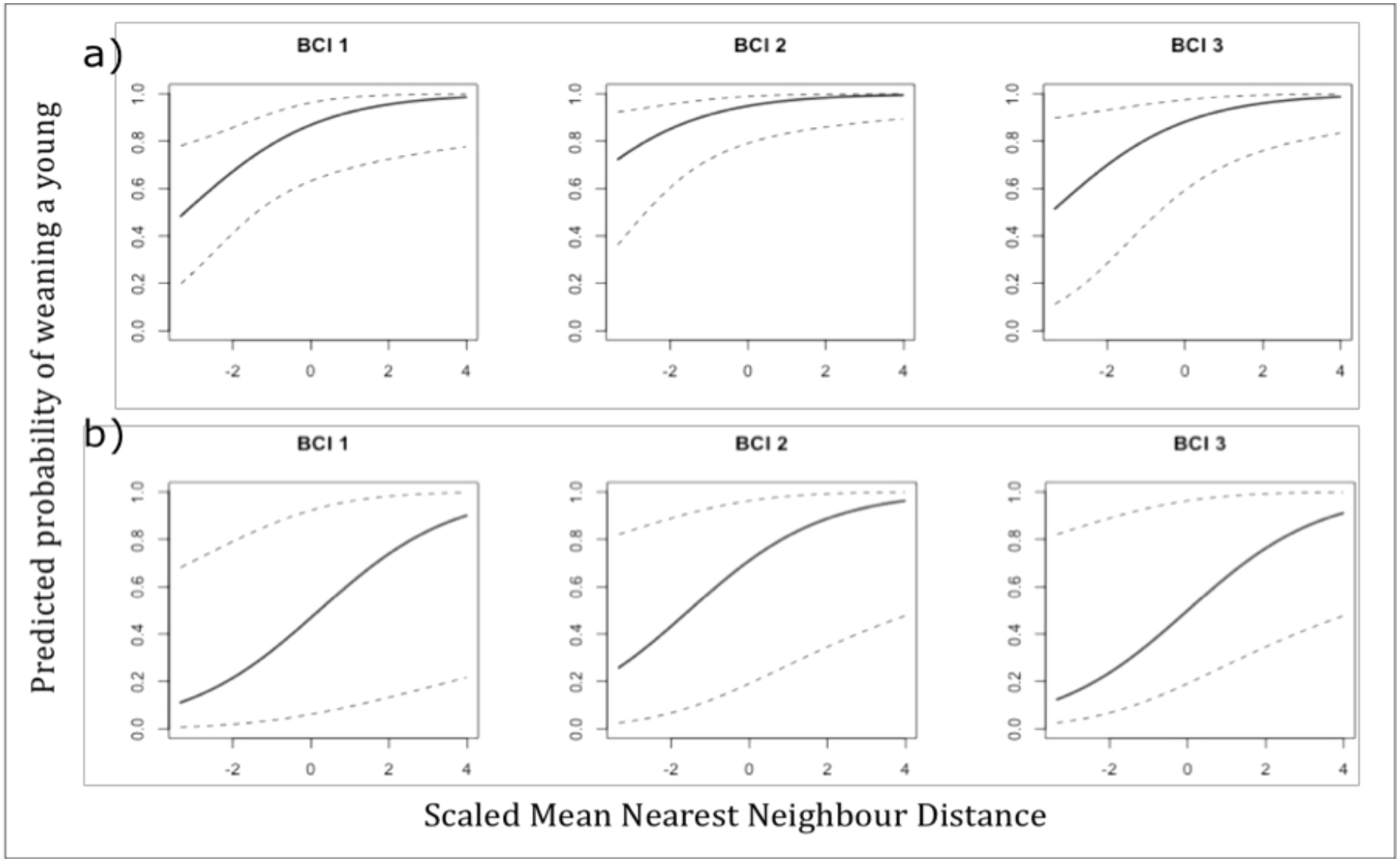

a)
Time A
Time B
Time C
b)
Time A
Time B
Time C
Predicted probability of weaning a young
0.0
0.2
0.4
0.6
0.8
1.0
-5
0
5
10
15
Scaled Number of Preferred Associates

Figure 3


a)
BCI 1
BCI 2
BCI 3
b)
BCI 1
BCI 2
BCI 3
Predicted probability of weaning a young
Scaled Mean Nearest Neighbour Distance

Supplementary Material

Principal components analysis of yearly social network measures (Approach 1)

a)

	PC1	**PC2**	PC3	PC4	PC5
Standard Deviation	**1.9247**	**0.8996**	0.5761	0.3615	0.1537
Proportion of Variance	**0.7409**	**0.1618**	0.0664	0.0261	0.0047
Cumulative Proportion	**0.7409**	**0.9028**	0.9691	0.9953	1

b)

	PC1	**PC2**	PC3	PC4	PC5
Strength	**-0.4980**	0.1053	-0.1831	0.6442	0.5408
Eigenvector	-0.3521	**0.7379**	0.5323	-0.2178	-0.0281
Reach	**-0.5074**	-0.0109	-0.2833	0.1927	-0.7906
Clustering	-0.3711	**-0.6532**	0.6600	-0.0013	0.0104
Affinity	**-0.4826**	-0.1331	-0.4090	-0.7074	0.2857

Table S1: Output for principal components analysis of five social network metrics generated by SOCPROG2.4 for 126 female kangaroos over four individual years (Approach 1). a) The importance of each component in explaining the variance in the data set. PC1 and PC2 together explained over 90% of the variance, and scores for individuals on each of these components (hereafter named Soc1 and Soc2 respectively) were generated. b) Loadings of the five social network metrics (Strength, Eigenvector Centrality, Reach, Clustering Coefficient and Affinity) onto each of the principal components. Rotations of approximately 0.5 and higher (in either direction) for PC1 and PC2 are shown in bold.

Principal components analysis of social network measures spanning two years (Approach 2)

a)

	PC1	**PC2**	PC3	PC4	PC5
Standard deviation	**1.9331**	**0.9207**	0.5181	0.3571	0.1392
Proportion of Variance	**0.7474**	**0.1696**	0.0537	0.0255	0.0039
Cumulative Proportion	**0.7474**	**0.9169**	0.9706	0.9961	1

b)

	PC1	**PC2**	PC3	PC4	PC5
Strength	**0.4980**	-0.1112	0.1005	-0.6520	0.5517
Eigenvector	0.3427	**-0.7628**	-0.4584	0.2998	-0.0252
Reach	**0.5057**	-0.0209	0.3136	-0.2165	-0.7737
Clustering	0.3870	**0.6065**	-0.6913	0.0393	-0.0547
Affinity	**0.4787**	0.1935	0.4512	0.6607	0.3056

Table S2: Output for principal components analysis of five social network metrics generated by SOCPROG2.4 for 110 female kangaroos over three overlapping two-year time periods (Approach 2). a) The importance of each component in explaining the variance in the data set. PC1 and PC2 together explained over 90% of the variance, and scores for individuals on each of these components were generated. b) Loadings of the five social network metrics (Strength, Eigenvector Centrality, Reach, Clustering Coefficient and Affinity) onto each of the principal components. Rotations of approximately 0.5 and higher (in either direction) for PC1 and PC2 are shown in bold.

Time periods for data collection of variables analysed in survival of each young

a)

Variable	Data used from the following months:	Mean (Range)
Rainfall (mm)	Sum of three months prior to month of LPY (mLPY)	155 (51.6 - 373.6)
Mean Group Size	Average of three months prior to month of LPY	6.42 (1.67 - 15.13)
# of Sightings	Sum of seven months prior to month of LPY	41.8 (15 - 81)
Mean NN Distance	Average of three months prior to month of LPY	6.23 (3.06 - 10.44)
BCI	Month of LPY	(1- 3)

b)

Variable	Data used from the following months:	Mean (Range)
Rainfall (mm)	Sum of mLPY and two prior months	168 (51.6 - 373.6)
Mean Group Size	Average of mLPY and two months prior	6.34 (1.67 - 15.13)
# of Sightings	Sum of seven months prior to mLPY	42.9 (15 - 81)
Mean NN Distance	Average of mLPY and two prior months	6.44 (4.08 - 10.72)
BCI	Month of LPY	(1- 3)

c)

Variable	Data used from the following months:	Mean (Range)
Rainfall (mm)	Sum of three months prior to month of PEP (mPEP)	182 (51.6 - 373.6)
Mean Group Size	Average of mPEP and two months after	5.44 (1.5 - 11.54)
# of Sightings	Sum of mPEP and six months after	41.7 (15 – 82)
Mean NN Distance	Average of mPEP and two months after	6.97 (3.67 – 11.00)
BCI	Month of PEP	(1- 3)

Table S3: Explanatory variables used in mixed model analyses of survival of each young (Approach 3). Data for each of the continuous or categorical variables were taken from the time periods specified for a) survival to LPY stage, b) survival to PEP, and c) survival to weaning. BCI = body condition index, Mean NN Distance = mean distance of a female's nearest neighbour when encountered in a group of two or more animals during social association surveys.

Chapter 6 – General Discussion

Overview

The main objective of my PhD was to study how the interactions between social structure and individual differences in personality related to fitness in a mammal with higher fission-fusion dynamics, using the eastern grey kangaroo as a model study species. I used observational data and in-field experimental tests to examine the relationships among these variables over a period of four years, over which environmental conditions and population demographics varied considerably. My work aimed to address two broad topics: which measures contribute to the strengths and patterns of females' social relationships, and what are the likely causes and consequences of individual variation in females' sociability measures. I have shown that individual differences in the personality dimensions of boldness and sociability were consistent over multiple years. However, similarity in boldness did not seem to be driving females' association patterns (Chapter 2). One factor that did moderately correlate with pairs' association strengths was their mother-daughter relationship status, which explained more variation in social patterns than did biparental relatedness estimates (Chapter 3), although most associations in the population were among females not closely related to one another. At a shorter temporal scale, rainfall influenced females' aggregation patterns, and individual females' body conditions and reproductive states were related to females' choosiness of their social grouping partners (Chapter 4). Ultimately, in this population, females that were highly sociable incurred costs to their reproductive success (Chapter 5), making the adaptive benefit of social integration in this species still unexplained. Each of these chapters discussed the findings of my analyses in detail; below, I discuss the findings of my research as a whole in the context of broader theoretical frameworks, and suggest future directions for this research into kangaroo social organization. My findings are discussed here in two main sections. The first covers what factors influence pairwise associations among female kangaroos over time and varying ecological conditions (investigated in Chapters 2 and 3), while the second covers what contributes to individual differences in sociability, and what the consequences of these individual differences are (investigated in Chapters 4 and 5).

Factors that could affect association patterns among females

Eastern grey kangaroos exhibit high fission-fusion dynamics in their social organization, joining and leaving temporary foraging groups that frequently change in size and composition. Despite this form of sociality, relationships among females have been shown to be more differentiated than expected if animals associated at random (Best et al. 2013). Some pairs associate more frequently

than would be expected based on overlap in their foraging ranges or spatial proximity (Stuart-Dick 1987; Carter et al. 2009; Best et al. 2014), a pattern that has also been reported in some other species with higher fission-fusion dynamics (Frère et al. 2010; Carter et al. 2013b; Strickland et al. 2014). For eastern grey kangaroos, which demonstrate social preferences by grazing in close proximity to one another, but do not engage in complex cooperative behaviours, females would not be expected to gain inclusive fitness benefits (Hamilton 1964) from preferentially associating with kin. Indeed, biparental relatedness has been previously shown to correlate only minimally with females' association strengths in kangaroos (Best et al. 2014; King et al. 2015), and this weak relationship has been suggested to be a passive phenomenon arising from female natal philopatry (King et al. 2015). Therefore, questions remain about the factors that influence why females choose to associate with particular other females (and, ultimately, what the adaptive benefits of such relationships are), as differentiated from factors that relate to aggregating with conspecifics in general.

When interpreting the patterns of animal associations, however, it is important to be mindful of the limitations of the data collection method used. Although the survey or census approach used in this study provides a regular 'snapshot' of information about number, spacing, and identities of females within a group, we make two broad assumptions in using such data to infer social associations. The first is that animals observed in close proximity are associating, rather than aggregating at a common resource. This assumption should be treated with caution when animals are grouped at point resources (such as the water sources and mineral licks within our study site), but since the majority of our survey observations occurred while kangaroos were grazing on an evenly distributed food resource, we can be more confident that most groups recorded were not simply aggregations. Furthermore, Farine (2015) argues that observations of individuals in the same place at the same time are more likely to accurately represent patterns of associations in species with higher fission-fusion social systems (such as eastern grey kangaroos) than in species with stable and fully-connected social groups, presumably because individuals in species with higher fission-fusion dynamics can make active choices about who to associate with. On a similar note, however, our analyses assume that animals observed together are displaying affiliative, rather than agonistic, behaviour. A potential future approach could consider combining survey data with information from focal animal samples (for example, on affiliative and agonistic acts) to generate a more complete picture of kangaroos' social relationships, although clear interactions of these kinds are not common in this species. The second assumption made is the use of the 'gambit-of-the-group' approach, in which each individual within a group is considered to be in association with every other group member (Whitehead and Dufault 1999). Although the 15-metre chain rule first

implemented by Jarman (1987) has been used in the present study and by others to define a group in this species, in reality groups defined in this way can involve from two to dozens of animals, and groups may have various degrees of dispersion. In large group arranged linearly, it is not certain that individuals at opposite ends would be close enough to respond to each others' behavioural cues or recognize each other. Future research should test the validity of this definition of a group, and aim to consider what is a meaningful measure of a foraging group to the study animal.

The work presented in Chapter 3 of this thesis suggests that a considerable proportion of the positive (yet weak) relationship between kinship and association strengths is explained by the post-weaning associations of mothers with their daughters. The strength of this post-weaning relationship is likely to vary among individual pairs (due perhaps in part to the ages of both the mother and the daughter) and among different populations. Mother-daughter associations were close and long-term in the lower-density Wallaby Creek kangaroo population (Jarman 1994), but in the higher-density population studied by King et al. (2015) females' association strengths were only weakly correlated with their relatedness estimates. The fitness benefits to a female kangaroo of associating with her daughter or her mother are likely to depend on the population density. In other group-living species, population density has been shown to influence social organization (for example, in yellow-bellied marmots (*Marmota flaviventris*), reviewed by Blumstein 2013), and density can also influence relationships between genetic relatives. Female red deer (*Cervus elaphus*) associated less frequently with female kin, and more frequently with unrelated conspecifics, at higher population densities (Albon et al. 1992). Both group density and group size have been positively linked to population density in eastern grey kangaroos (Southwell 1984), and changes in these measures could have implications for individuals' sociability metrics. At the Wallaby Creek kangaroo site, daughters who had their mothers present in the population (with whom they presumably associated, although association strengths were not analysed) began reproducing earlier and had greater survival of their young than did daughters without mothers present (Jarman 1994). The mechanisms that could explain this are unclear, as female kangaroos do not exhibit cooperative behaviours. However, a study of an herbivorous placental mammal, the bison (*Bison bison*), found that weaned calves that grouped with their mothers spent more time in the center of a foraging group, and were displaced by conspecifics less often (Green et al. 1989), suggesting potential energetic and safety benefits to post-weaning associations between mothers and daughters. Future work on kangaroos could explore if similar benefits to either foraging or reproduction are conferred to daughters by their associations with their mothers, and whether the extent of these benefits is dependent upon population density.

Although not measured in the current study, another ecological variable known to influence animal social patterns is real or perceived predation pressure. Guppy (*Poecilla reticulata*) social networks were more stable, and ties between individuals were stronger, under greater predation risk (Kelley et al. 2011). Predation can also relate to animals' group sizes, and may encourage the formation of larger groups that dilute the risk of predation for individual animals, or smaller groups that are less likely to be detected by a predator (e.g. Hebblewhite and Pletscher 2002). In a study population of eastern grey kangaroos at Brindabella Ranges, mean group sizes of eastern grey kangaroos decreased significantly during a period of predator control (Banks 2001). Since we did not collect information on predator abundance at our study site we could not incorporate such data into our analyses of kangaroo grouping patterns and other dimensions of sociability, but future research could incorporate predator call playbacks or odour cues to investigate the influence of predation risk on these measures.

An additional variable that I had hypothesized might relate to females' association patterns was similarity in personality measures, since homophily or social assortment based on personality has been observed in other group-living species (e.g. Croft et al. 2009; Massen and Koski 2013; Morton et al. 2015). Furthermore, breeding partners with similar personalities can have higher reproductive success than those with dissimilar personalities (Schuett et al. 2011; Rangassamy et al. 2015). Species that receive an anti-predator advantage from aggregating may additionally benefit from displaying behavioural similarity to group mates (reviewed by Webster and Ward 2011). Among adult and sub-adult female kangaroos, we observed a moderately significant correlation between association strengths and similarity in boldness in one two-year time period, but no significant assortment in the following two years (Chapter 2). Although female offspring were born and weaned all throughout the four-year study period, the proportion of females that had weaned daughters at the end of the first two-year time period was higher than at any other time – approximately one third of the females included in these analyses of social assortment had a sub-adult daughter in the population by the beginning of the second time period. It is possible that during this later time period, mothers preferred to associate with their sub-adult daughters rather than with other adult females to whom they were similar in boldness, and mothers without daughters of this age may select their associates based more on similarity in personality. This pattern could explain the differences in social assortment between time periods. Although we did not consider the relative importance of similarity in boldness and pairwise genetic relatedness on females' association strengths in this study, it would be interesting to test in future analyses which of these variables explained a greater proportion of association strengths. This could be approached statistically by using a partial Mantel test, or alternatively we could compare females who did and

did not have sub-adult daughters in the population, and examine the similarity in boldness of females to their associates between groups.

Preferential associations among females, in which individuals go out of their way to be with one another, were not related to pairs' similarity in boldness. In the two-year period when we found a positive relationship between pairwise association strength and similarity in boldness, there that there was no significant association between whether pairs were preferred associates and their similarity in boldness. Neither did we find support for the existence of 'social niches' (e.g. Bergmüller and Taborsky 2010; Montiglio et al. 2013) based on boldness among these individuals. According to the social niche hypothesis for the origin and maintenance of individual differences in personality, I would expect that pairs of kangaroos that associated frequently would have more dissimilar personalities as a way of reducing social competition. Since the non-invasive nature of our study prohibited experimental re-arrangement of groups (and this would in any case be logistically difficult in a population with open membership temporary foraging groups), it would not be possible to experimentally test if pairs become more different in their personalities with increased exposure. Such an experiment could potentially be performed in captivity, as shown by a recent study showing greater individual variation in personality types among group members with higher familiarity in social spiders (*Stegodyphus mimosarum*) (Laskowski and Pruitt 2014). However, it is possible that individuals may have less need to adopt social niches to reduce group competition in species that have higher fission-fusion dynamics (such as the eastern grey kangaroo) than in species that live in stable groups (as suggested by Laskowski and Bell 2014), since higher fission-fusion dynamics can already help to mitigate costs of group living (which include increased competition) in some species (Lehmann et al. 2007).

Possible causes and consequences of individual differences among females

We have shown that although females' patterns of aggregation and associations varied with both environmental and intrinsic short-term variables, individual females exhibited significant consistency in measures of their sociability (and boldness) over periods of a year or longer. Overall, females' boldness (as measured by flight initiation distance, FID) was highly repeatable over four years, although at the individual level there was variation in repeatability among FID measures. Incorporating the concept of individual plasticity into the study of animal personality is becoming increasingly recognized to be important (Dingemanse et al. 2010). Although my thesis did not address the factors relating to individual plasticity in boldness, this should be examined in further studies. Another aspect of the personality measures studied that I did not address was heritability

estimates. Boldness has been shown in some studies to have significant heritability (van Oers et al. 2004; Ariyomo et al. 2013), indicating that a genetic basis explains some proportion of personality variation in the species studied. Among the female kangaroos in our study population, there were at least twelve pairs in which both a mother and her daughter were tested for boldness within the same two-year time period. Although these sample sizes would likely be too small for traditional analyses of heritability of a trait, and paternity is not known in our population, it would be interesting to explore whether mothers and daughters were more similar in boldness than were age-matched unrelated pairs of females. However, it would be difficult to separate the influences of genetic and maternal social effects on individuals' temperaments, without being able to conduct cross-fostering experiments and without knowledge of paternal behavioural phenotypes. Macropods have been previously used for cross-fostering studies in captivity (e.g. Taggart et al. 2005), so such a study might be feasible, but capturing females in our study population in order to conduct such an experiment would likely have unintended effects on other aspects of females' behaviour.

When testing for boldness in the field, we could not experimentally manipulate the sizes and compositions of groups in which individuals were tested for FID. However, our methods tested animals in their social contexts in the wild, hence individuals' responses were likely to reflect ecologically significant behaviour. Researchers are becoming increasingly aware that individuals of social species may express their personalities differently when tested in isolation than when tested with conspecifics (van Oers et al. 2005; Mainwaring et al. 2011; Webster and Ward 2011), yet personality tests on individuals from wild populations are rarely conducted in the species' natural social settings. An interesting area for future studies would be to investigate whether females differ in their FIDs when foraging in a group with close associates, or with preferred associates, compared to when foraging with casual associates. As shown in male cichlid fish, individuals can respond to behavioural tests differently when in the presence of a familiar compared to an unfamiliar conspecific (Galhardo et al. 2012), so it is possible that kangaroos may also exhibit different levels of boldness depending on the strengths or quality of their relationships with those in their temporary foraging group. We did not record the identities of the target female's nearest neighbour or group mates when conducting the FID tests in the field, although if these studies are repeated in the future, they could incorporate such data into the analyses of variables affecting FID. At a different study site, kangaroos that grazed next to a close associate devoted more time to feeding than did females grazing next to a less familiar social partner (Carter et al. 2009), so it is possible that the social environment modulates females' expression of other personality measures.

When testing for boldness using the FID method, we were aware of the concerns in the literature that using a single measure to assess a personality trait can be problematic (Beckmann and Biro 2013). Early on in my fieldwork I conducted pilot studies of other tests that could be used to experimentally assess boldness, but no methods proved feasible. In addition, I had approximately four hours each day during which to collect all field data, because the kangaroos rested in cover most of the day, so my ability to conduct behavioural tests was limited by time availability. Perhaps future studies could employ a different test for this behavioural trait to validate whether boldness as measured by FID corresponded to other measures of boldness. Additional tests would need to exclude the use of novel objects, as cautioned by Carter et al. (2012), because such tests may measure exploratory tendency rather than boldness. One possibility would be to measure individuals' latency to resume feeding after a threatening stimulus or startle, a variation on the emergence test that has been used to measure boldness in other species (Carter et al. 2013a). Difficulty would exist in targeting this kind of stimulus to particular individuals (if, for example, predator playback calls were used), but it could still be considered for future work.

In addition to showing individual consistency in boldness, I showed that female kangaroos differed consistently in several measures of their sociability over periods of a year or more. In Chapter 4 we considered the short-term variables that might constrain various aspects of female's sociability. Although we found significant relationships between sociability measures and individuals' body conditions and reproductive states, we could not consider all potential variables that might affect females' aggregation tendencies and social relationships. It is possible that the numbers of close relatives that females had within the population could influence their patterns of sociability. Some mothers and daughters continued to associate frequently even when the daughters had reached breeding age (Chapter 3), so aggregation patterns or numbers of social bonds may be different for females that associated closely with their mother (or daughter) and those that did not. It is also possible that some maternal half-sisters (especially those close in age) have strong associations with one another, although we did not explicitly test for this. It would be interesting to explore whether measures of sociability – such as preferred group size, number of preferred associates, and social network-based metrics – varied among females with different numbers of close maternal relatives in the population.

Over short-term periods of single months, we observed that food availability, body condition, reproductive state, and in some cases interactions between these variables, influenced adult females' grouping and association tendencies. We also found, on a longer time-scale, that females with a smaller number of preferred associates were more likely to wean a young in a year (Chapter

5). In our study, we did not investigate how our short-term sociability measure of number of grouping partners used in Chapter 4 related to the longer-term sociability measure of number of preferred associates used in Chapter 5. It would be interesting to investigate this, and also to test whether individuals showed consistent differences in their numbers of grouping partners (when controlling for mean group size) across different months/states. We also found that females scoring highly on a principal component representing their social network size were less likely to wean a young in a year (Chapter 5), but, again, we have not explored how an individual's number of different group members in a month might relate to their social network measures.

There are potential problems with the use of social network metrics in species exhibiting high fission-fusion dynamics. Recent work by King (2015) on a different population of eastern grey kangaroos showed that sample size (i.e. the number of observations of an individual) was significantly positively related to scores on all social network measures except for clustering coefficient. This phenomenon may create a potential confounding factor when investigating other correlates of individuals' social network metrics. Although this has not been formally tested in the Sundown kangaroo population, the influence of sample size on individuals' measures of sociability should be considered in future work and statistical methods should be developed to deal with this issue. Increasing the cutoff for the number of times individuals needed to be observed on association surveys to be included in social network analysis may help somewhat to address this issue (Whitehead 2008), although omitting individuals seen less frequently could mask subtle patterns of associations.

The relationship between sociability and boldness reported in female kangaroos in the current study (and possible relationships between sociability and other personality dimensions not investigated in this study) is also important to consider as a potential influence on females' sociability. A boldness-sociability behavioural syndrome, in which traits are correlated across contexts and situations (Sih et al. 2004), may constrain individuals from adopting optimal social strategies required for maximum fitness in a given circumstance. These two personality measures may both be linked to the same underlying genetic or physiological cause. Boldness may be also be linked to individuals' exploratory tendency or their activity level, which are both traits considered to be key axes of animal personality (Réale et al. 2007). A possible future direction would be to conduct focal observations to examine the rates at which individuals join and leave temporary foraging groups, to see how these relate to measures of boldness and/or sociability. This could allow us to test possible explanations for the observed relationship between boldness and the preferred group size aspect of sociability. Bolder females may be more likely than shyer females to leave foraging groups once

they get too large, similar to the pattern observed in sheep (*Ovis aries*) (Michelana et al. 2009), as shy individuals may perceive the risks of changing groups differently to bold individuals.

Another variable that was not considered in the current study but that might relate to individual variation in personality traits is parasite load. Parasitism is increasingly being considered as a variable that can influence the evolution of personality (Barber and Dingemanse 2010), potentially helping to maintain consistent individual differences within a population. Eastern grey kangaroos can host many species of internal parasites (Beveridge and Arundel 1979), so the relationship between parasite loads and personality traits may be an interesting direction for future studies. Variation in parasite loads among the female kangaroos studied may have contributed to differences in body condition among individuals – especially considering that body condition was not entirely dependent on lagged rainfall, a proxy for food availability used in Chapter 4. Although the conditions of all kangaroos tended to be poorer during prolonged dry spells, some females still had poor body condition in times of high lagged rainfall, which could possibly be due to high parasite loads. Females that need to spend more time grazing to compensate for the reduced nutrient absorption caused by intestinal parasites would have less time available for the formation and maintenance of social relationships (Dunbar et al. 2009), strengthening the trade-off between sociability and resource acquisition.

In conclusion, my research has contributed to our understanding of kangaroo social behaviour, while also addressing questions about the relationships between sociability and fitness in mammals in general. Understanding how individual variation in personality traits, including sociability, relates to fitness measures continues to be a key area of interest in behavioural ecology. The directions for future research discussed above could help demonstrate how group living mammals balance the costs and benefits of various dimensions of personality under variable environmental conditions.

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